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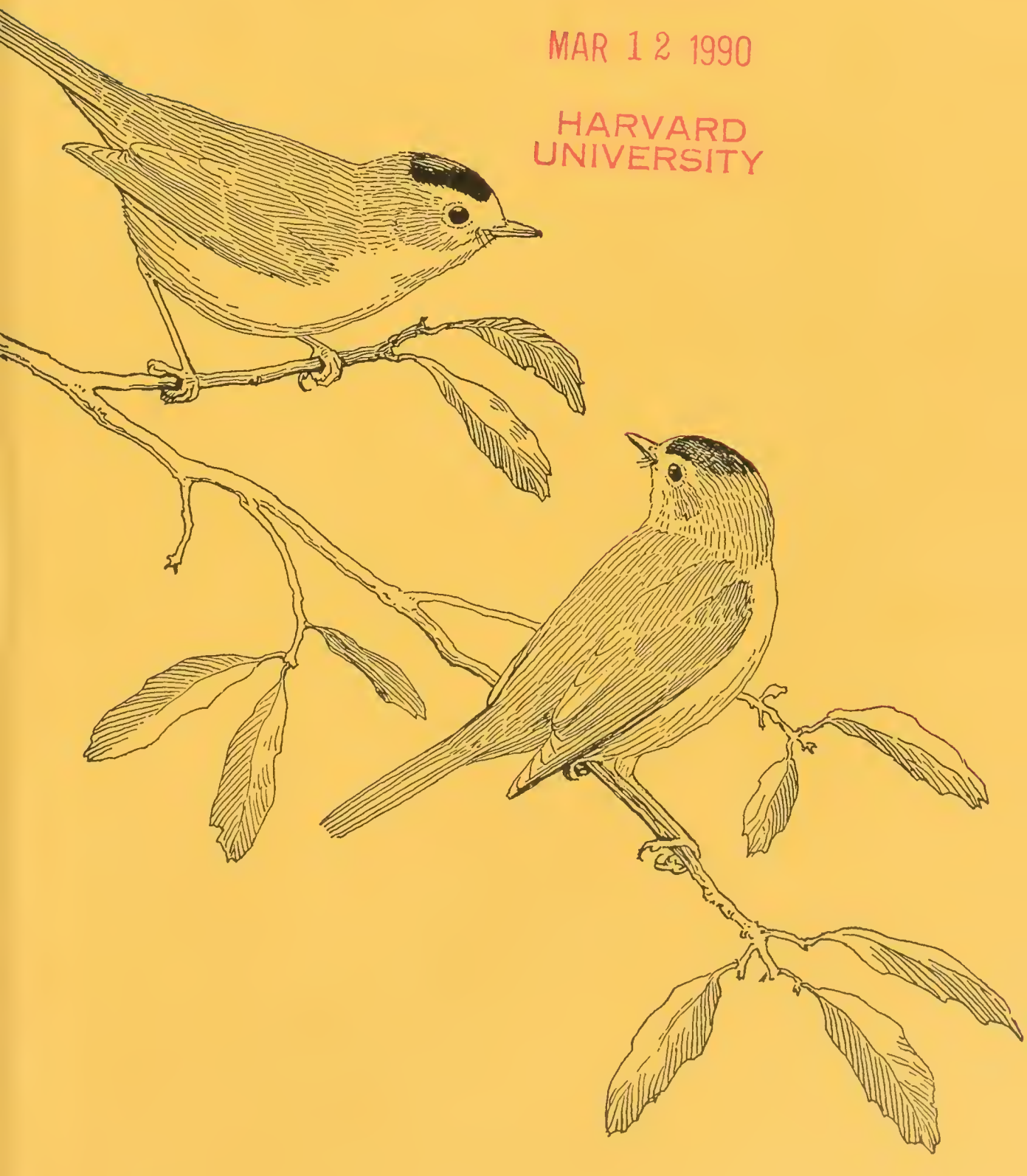

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The Colima Warbler (*Vermivora crissalis*) compared with its close relatives, as seen in adult males in fresh fall plumage from the Smithsonian Institution collection. From top to bottom are the Nashville Warbler, (*V. ruficapilla*), Virginia's Warbler (*V. virginiae*), and the Colima Warbler. These three species are similar in their "plisk" call-note, their habitat, and their nest upon the ground. Notice the large size and comparatively long tail of the Colima Warbler and the gray overlying the green back of the Nashville Warbler, whose yellowish rump distinguishes it as the western race, *ridgwayi.* Painting by Joe T. Marshall.

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RANGE AND HABITAT OF THE COLIMA WARBLER

DIRK V. LANNING,[1] JOE T. MARSHALL,[1] AND JAMES T. SHIFLETT[2]

ABSTRACT.—We surveyed the breeding range of the Colima Warbler (*Vermivora crissalis*) in northeastern Mexico and western Texas between April and June 1983 and located 167 Colima Warblers within an area that included Coahuila, Nuevo Leon, Tamaulipas, and Texas—states where they previously were known to occur. In addition, we observed 13 warblers in San Luis Potosi and Zacatecas. We found Colima Warblers at elevations between 1800 and 3000 m in oak-pine (*Quercus* spp. and *Pinus* spp.) habitat with bunchgrass (*Muhlenbergia* spp.) ground cover.

Colima Warblers also were observed in their winter range in west-central Mexico during February 1983. We found eight Colima Warblers in Jalisco and Michoacan in oak-conifer habitat at 2400 to 3000 m elevation. These are the first published observations of Colima Warblers in western Mexico since 1963.

Breeding habitat at 180 plots where Colima Warblers were sighted was compared with 24 unoccupied plots of oak-pine vegetation. Colima Warblers used sites where the trees were shorter ($\bar{x}$ = 8.1 ± 4.0 [SD] m), the shrubs were taller ($\bar{x}$ = 2.30 ± 0.80 m), and the ground vegetation was taller ($\bar{x}$ = 0.63 ± 0.29 m) relative to unoccupied sites. The species used areas where the shrub cover was greater ($\bar{x}$ = 42 ± 22%) and the ground vegetation (≤1 m tall) cover was greater ($\bar{x}$ = 51 ± 22%) relative to unoccupied plots.

Colima Warblers often foraged and perched in the dense, lower vegetation in both breeding and winter habitats. The tree, shrub, and ground vegetation strata were often contiguous. Colima Warblers were found in undisturbed sites and in areas of light-to-moderate grazing, selective logging, and burning. *Received 19 Dec. 1988, accepted 9 March 1989.*

The Colima Warbler (*Vermivora crissalis*) is known during the breeding season from only a few locations in northeastern Mexico in the states of Coahuila (Bangs 1925, Burleigh and Lowery 1942, Urban 1959, Ely 1962, Wauer and Ligon 1977), Nuevo Leon (Miller et al. 1957, Hubbard and Crossin 1974), and Tamaulipas (Griscom 1923, Bangs 1925). It is known

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from a single location in the United States—the Chisos Mountains of Texas (Van Tyne 1929, Wauer 1973).

The American Ornithologists' Union (AOU 1983) summarizes the Colima Warbler breeding habitat as thickets and scrubby woodland, primarily oak (*Quercus* spp.), maple (*Acer* spp.), cypress (*Cupressus arizonica*), and juniper (*Juniperus* spp.) scrub in hilly areas. Descriptions of the Colima Warbler's breeding habitat in Mexico are limited (Burleigh and Lowery 1942, Ely 1962, Hubbard and Crossin 1974). The habitat, insectivorous food habits, and ground nests of Colima Warblers in Texas are described by Van Tyne (1936), Van Tyne and Sutton (1937), Blake (1949), Snyder (1957), Gehlbach (1967), Wauer (1973, 1979), and Oberholser and Kincaid (1974).

The Colima Warbler winters in west-central Mexico from southern Sinaloa south through Jalisco, Colima, and Michoacan to Guerrero (AOU 1983). The last published record of a Colima Warbler in west-central Mexico was by Schaldach (1963), who collected one bird during October, 1958, in Jalisco in fir (*Abies religiosa*) forest. Winter habitat includes open woodland, thickets, and scrub (AOU 1983).

The Colima Warbler is closely related to the Nashville Warbler (*V. ruficapilla*) and the Virginia's Warbler (*V. virginiae*; see Frontispiece); together they constitute a superspecies (Mengel 1964, Stein 1968, Mayr and Short 1970, Brush and Johnson 1976, AOU 1983). Phillips et al. (1964) considered them a single species.

During nine weeks from April to June 1983, Lanning and Marshall searched for Colima Warblers in the Sierra Madre Oriental in northeastern Mexico and Texas. Their objectives were to locate and observe these birds in selected areas throughout their previously established and suspected breeding range, describe their habitat, and evaluate threats to their habitat. During two weeks in February 1983, Lanning and Shiflett located and observed Colima Warblers in parts of the warbler's known winter range in the Trans-volcanic Belt in Jalisco and Michoacan.

STUDY AREAS

The Sierra Madre Oriental is the prominent mountain range in northeastern Mexico. The northern half of this range, terminating in western Texas, is a series of isolated mountains and ridges <3000 m in elevation. The southern half of this range, extending to the Trans-volcanic Belt of central Mexico, is a nearly continuous massif ranging from 50 to 100 km wide, with elevations up to 3700 m. In the Trans-volcanic Belt in Jalisco and Michoacan there are numerous volcanic peaks, some with elevations >4000 m.

Three major biotic communities occur in these montane areas (classification in Brown et al. 1979, and a thorough description in Brown 1982): Interior Chaparral consists of short oaks and a variety of other shrubs and compact trees; Madrean Evergreen Woodland is

dominated by a variety of oaks and pines (*Pinus* spp.); and Madrean Montane Conifer Forest is dominated by pines and other conifers. The biotic communities intergrade locally.

The climate in the Sierra Madre Oriental during the spring is warm and sporadically wet. Temperatures generally range between 10 and 25°C. In southeastern Coahuila, 71% of the precipitation (390 mm at San Antonio de las Alazanas) falls between May and October (Instituto de Geografia, Univ. Nac. Auton. Mex. 1975). Daily maximum temperatures in the Chisos Mountains average about 30°C during the five warmest months, and most precipitation comes between May and October (400 mm average in the Chisos Basin; Wauer 1973). In the Trans-volcanic Belt, winters are usually dry with temperatures between −5 and 25°C.

METHODS

Before field work we surveyed museum specimens and pertinent literature to locate Colima Warbler records. We communicated with individuals who had observed Colima Warblers in Mexico.

Breeding season survey.—From April to June we visited locations and habitats where Colima Warblers had been collected or observed, as well as additional regions and habitats where they had not been observed. During the first five hours each day, we looked for birds while we walked along trails, roads, ridges, valleys, and up and down slopes. Each time we located a Colima Warbler, we collected data on its activity, position in the habitat, geographic location, and the characteristics of the terrain and vegetation. Elevations (above sea level) were determined from topographic maps (Cartas Topografica; 1:250,000 scale). We measured slope direction with a compass and estimated slope angle. We visually estimated the location and extent of oak and conifer vegetation with the aid of vegetation maps (Cartas Uso del Suelo; 1:1,000,000 scale). The series of topographic and vegetation maps were obtained from the Secretaria de Programacion y Presupuesto of the Mexican government.

We described vegetation characteristics at 180 Colima Warbler sites, with each vegetation plot centered at the point where we first observed the bird. Canopy coverage of trees (>3 cm diameter at breast height [dbh] and >1 m tall) was measured with a spherical densiometer (Lemmon 1956). We took sightings in four directions from the center of each plot and averaged the results to provide a measurement of tree canopy cover within a 90° arc over the plot. We measured the height of the tree canopy foliage, using a tape measure for heights ≤4 m and visual estimates for heights >4 m.

The height of shrubs (≤3 cm dbh and >1 m tall) and ground vegetation (all the plants ≤1 m tall) and depth of litter layer were measured within a 2 m radius around the center of the plot. We made visual estimates of the canopy cover of each of the three layers.

We assessed the same vegetation characteristics with the same methods at 24 plots in areas where we were unable to locate Colima Warblers. We located the center of each vegetation plot in an area that appeared to be representative of the surrounding vegetation and terrain. All of the unoccupied plots were in oak-pine vegetation that contained shrubs and trees and within 4 km from where we observed Colima Warblers and at ≥1700 m elevation.

We compared vegetation characteristics at occupied plots and unoccupied plots using two-tailed *t*-tests. Before statistical comparison, the data were transformed (where necessary) to correct heteroscedasticity (Sokal and Rohlf 1981).

Winter observations.—During two weeks in February, we searched for Colima Warblers in and near areas where they previously were observed or collected. We looked for birds, usually in the morning, while walking along roads and trails. We collected data on each

Colima Warbler's activity and on the basic characteristics of the terrain and vegetation in the vicinity of the bird. We visually estimated the extent of oak and conifer vegetation within the winter range of the Colima Warbler with the aid of the vegetation maps from the Mexican government.

RESULTS

Breeding season survey.—We located 167 Colima Warblers in oak-pine habitat in the four states where they previously were known to occur (Fig. 1). We sighted 117 birds on nine different mountains (1800 to 3000-m elevation) throughout Coahuila, 35 birds along the main massif of the Sierra Madre Oriental (2150–2900 m) in southern Nuevo Leon, eight birds in the Sierra Madre Oriental (2200–2900 m) in southwestern Tamaulipas, and seven birds in the Chisos Mountains (2100–2300 m) in western Texas. Singing Colima Warblers were present in all of these areas.

We observed 13 Colima Warblers in oak-pine habitat in two states (Fig. 1) that were not part of their previously known breeding range. We found a pair of birds, including a singing male, on 17 May in the Sierra Catorce (2800 m) in northern San Luis Potosi. We observed four birds, including one singing male, on 12 May in the Sierra Concepcion del Oro (2600–2800 m) in northeastern Zacatecas. The following day, we found seven birds, including three singing males, in a part of the Sierra Encarnacion (2700–2800 m) in Zacatecas.

We checked several other areas surrounding the known geographic and elevation range of the species and were unable to locate additional Colima Warblers (Fig. 1). We searched two mountains in oak-pine vegetation west of the species' range, in the Sierra Rica (2000–2400 m) in northern Chihuahua and in the Sierra Parras (1900–2700 m) in southern Coahuila. We searched in the high pine forest (3400–3700 m), above the warbler's elevational range, on Cerro Potosi in Nuevo Leon. We examined four locations in oak-pine woodland and forest on the relatively humid and lush lower slopes of the Sierra Madre Oriental, east and south of the species' range: one site (1300–1600 m) in northern Coahuila, two sites (1000–1700 m) in southern Nuevo Leon, and one site (1300 m) in southwestern Tamaulipas.

Colima Warblers seemed to be common birds in suitable oak-pine habitat throughout much of their geographic and elevational range. During our morning transects (totaling 110 km) through chaparral, woodland, and forest vegetation, we observed an average of one Colima Warbler per 0.6 ± 0.7 [SD] km of transect. When the warblers were seen frequently, they were spaced about 100 to 200 m apart. We did not find them in meadows and areas that had been cleared for agriculture or dwellings.

Eight other species of breeding birds were common in the oak-pine

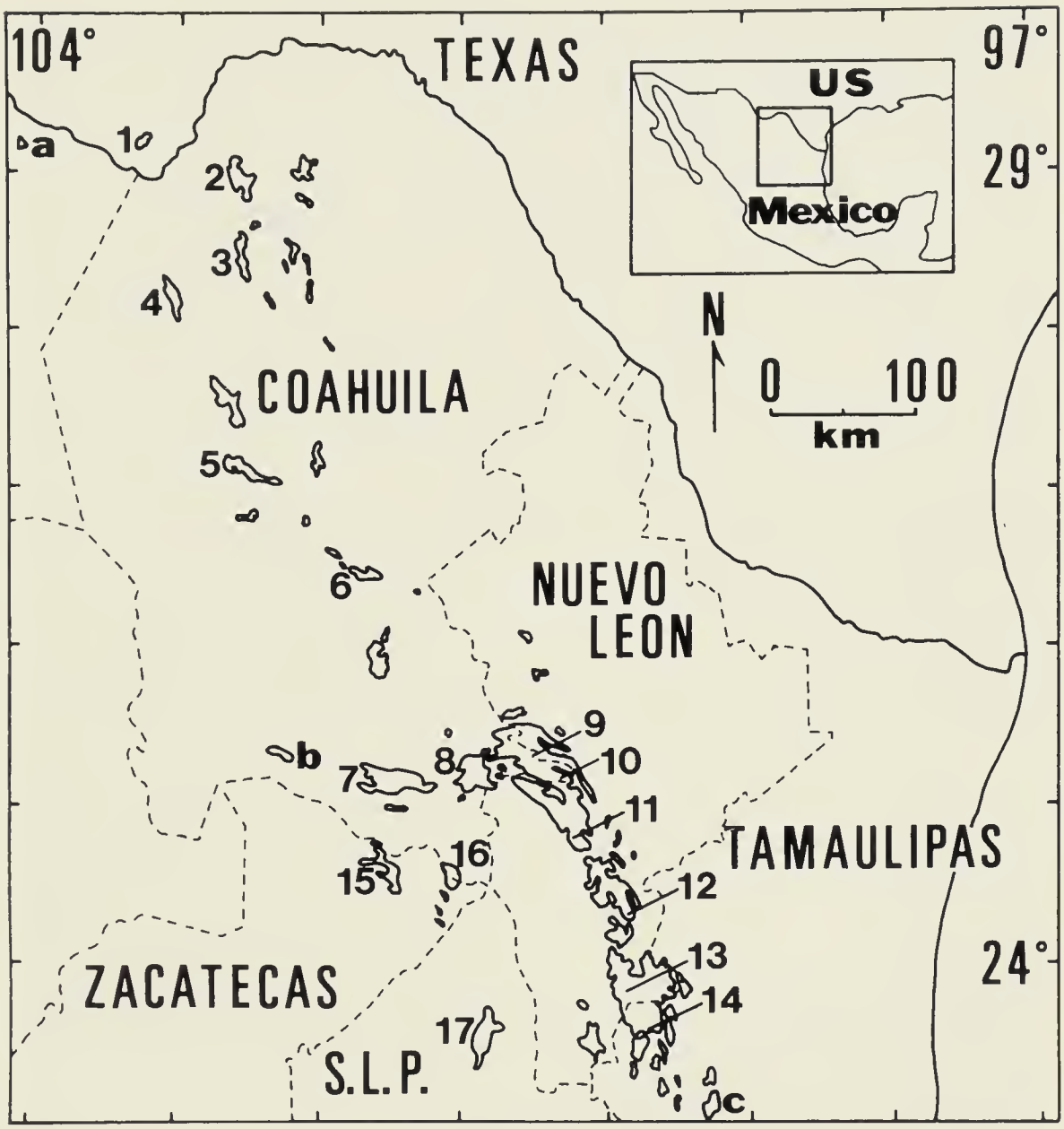

FIG. 1. Map of northeastern Mexico and adjacent United States showing the range of the Colima Warbler during the breeding season. Areas enclosed by solid lines indicate oak and conifer vegetation above 1800 m elevation. Numbers indicate areas where we observed Colima Warblers during spring 1983: (1) Chisos Mountains, (2) Sierra (S.) del Carmen, (3) S. la Encantada, (4) S. del Pino, (5) S. la Madera, (6) S. del San Marcos, (7) S. Guadalupe, (8) S. Zapaliname, (9) S. la Viga and S. Potrero de Abrego, (10) S. San Antonio and S. la Marta, (11) Cerro Potosi, (12) S. 4 km NE of Ascension, (13) S. Pena Nevada, (14) S. 5 km S and 10–15 km NE of Miquihuana, (15) S. 13 km W of Concepcion del Oro, (16) S. Encarnacion, and (17) S. Catorce in San Luis Potosi (S.L.P.). Letters indicate areas that were outside the warbler's breeding range: (a) S. Rica in Chihuahua, (b) S. Parras, and (c) S. de Guatemala.

habitat where we observed Colima Warblers: Broad-tailed Hummingbird (*Selasphorus platycercus*), Northern Flicker (*Colaptes auratus*), Gray-breasted Jay (*Aphelocoma ultramarina*), Bushtit (*Psaltriparus minimus*), Bewick's Wren (*Thryomanes bewickii*), Hutton's Vireo (*Vireo huttoni*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Yellow-eyed Junco (*Junco phaeonotus*). All were observed <1 km from Colima Warblers and on at least 21 of the 29 days that we saw Colima Warblers. The Brown-headed Cowbird (*Molothrus ater*), a potential brood parasite, was observed <1 km from Colima Warblers on only one of those days.

When first observed, 99 of the Colima Warblers were in oaks, 32 in pines, and the remaining 49 in other conifers and broad-leaf trees and shrubs. The warblers were either perched on or foraging among the vegetation. Ninety-two of the birds were singing. Most (N = 173) birds were surrounded by vegetation; only seven were first observed while perched on the highest, most exposed twigs. The birds were between 0.9 and 14 m ($\bar{x}$ = 4.2 ± 2.3 m) above ground, in trees (N = 150) and shrubs (N = 30) that were 1 to 22 m ($\bar{x}$ = 6.3 ± 3.5 m) tall. When foraging, Colima Warblers were usually gleaning small arthropods from leaves, twigs, and flowers. They occasionally caught flying insects.

Colima Warblers were observed at elevations between 1800 and 3000 m ($\bar{x}$ = 2505 ± 250 m). They were observed on slopes that varied from 0 to 90° ($\bar{x}$ = 30 ± 18°). Eighty-three warblers (47%) were sighted on northwestern, northern, and northeastern slopes. Slope direction where Colima Warblers were sighted was not uniformly distributed among the eight major compass points (N = 177 slopes >0°, χ^2 = 25.89, df = 7, P < 0.001). The oak-pine habitat used by the Colima Warblers was more abundant on northern exposures than on the more arid southern exposures.

Oaks were found in 178 of the 180 plots containing Colima Warblers (Table 1). The following species were identified by J. Tucker (pers. comm.; specimens collected by Marshall and deposited in the herbarium at the Univ. of Calif. at Davis): *Quercus glaucoides, Q. gravesii, Q. grisea, Q. hypoxantha, Q. intricata, Q. pringlei,* and *Q. saltillensis.* Pines and grasses, especially bunchgrasses (*Muhlenbergia* spp.), were the next most abundant plant categories and were each found in two-thirds of the plots (Table 1).

There were significant differences in the structure of the vegetation between the 180 plots containing Colima Warblers and the 24 unoccupied plots containing oak-pine vegetation (Table 2). Warblers used sites where the trees were shorter (P = 0.002), the shrubs were taller (P = 0.002), the ground vegetation (≤1 m tall) was taller (P < 0.001), and the litter (leaves and twigs) were deeper (P = 0.016) relative to unoccupied plots. The warblers used sites where the shrub cover was greater (P < 0.001) and

TABLE 1

PLANTS THAT OCCURRED ON AT LEAST 5% (9) OF THE 180 PLOTS WITH COLIMA WARBLERS

Plant category (representative species)	Percent of plots
Oak (*Quercus gravesii, Q. glaucoides, Q. pringlei*[a])	99
Grasses (especially *Muhlenbergia* spp. bunchgrasses)	68
Pine (*Pinus cembroides, P. montezumae, P. ponderosa*)	67
Annual flowering plants (Class Dicotyledonae)	44
Madrone (*Arbutus xalapensis*)	43
Juniper (*Juniperus deppeana, J. flaccida, J. occidentalis*)	23
Douglas-fir (*Pseudotsuga menziesii*)	22
Beargrass (*Nolina erumpens*)	17
Agave (*Agave macroculnis, A. palmeri, A. scabra*)	15
Sumac (*Rhus trilobata, R. virens*)	15
Arizona Cypress (*Cupressus arizonica*)	14
Ferns (Class Pteropsida)	12
Chokecherry (*Prunus serotina*)	12
Yucca (*Yucca baccata, Y. elata*)	11
Mountain-mahogany (*Cercocarpus montanus*)	10
Sotol (*Dasylirion wheeleri*)	9
Quaking Aspen (*Populus tremuloides*)	9
Buckbrush (*Ceanothus caeruleus, C. fendleri*)	8
Club Mosses (Class Lycopsida)	7
White Fir (*Abies vejari*)	6
Silktassel (*Garrya ovata*)	5

[a] See text for additional species of oaks.

the ground vegetation cover, especially bunchgrass, was greater ($P < 0.001$) relative to unoccupied plots. The tree, shrub, and ground vegetation strata in Colima Warbler habitat were often contiguous, with nearly continuous foliage from the ground to the top of the trees. In the plots where Colima Warblers did not occur, there was less shrub and ground vegetation cover, and the different vegetation strata were more disjunct.

Contiguous oak and conifer vegetation that contained Colima Warblers varied from habitat islands as small as 10 km^2 on isolated mountains to large expanses as large as 2000 m^2 in the main massif of the Sierra Madre Oriental.

Winter observations.—We found five Colima Warblers at two locations (2400 and 3000 m) on the Volcanes de Colima (19°35′N, 103°35′W) in Jalisco. We found three Colima Warblers at two locations (2400 and 2500 m) on Cerro Tancitaro (19°25′N, 102°20′W) in Michoacan. We did not hear any Colima Warblers sing, but we did hear their sharp call notes. We saw Colima Warblers that appeared to be alone and individuals in mixed-species flocks.

TABLE 2
CHARACTERISTICS OF THE VEGETATION IN 180 PLOTS WITH COLIMA WARBLERS AND 24 PLOTS WITHOUT COLIMA WARBLERS

Vegetation characteristic	Plots with Colima Warblers Mean ± SD	Plots without Colima Warblers Mean ± SD	P[a]
Tree canopy height[b] (m)	8.1 ± 4.0	11.6 ± 5.5	0.002
Shrub height[c] (m)	2.30 ± 0.80	1.75 ± 1.06	0.002
Ground vegetation height[d] (m)	0.63 ± 0.29	0.40 ± 0.26	<0.001
Litter depth (m)	0.06 ± 0.04	0.04 ± 0.03	0.016
Tree canopy cover (%)	70 ± 21	71 ± 24	0.660
Shrub cover (%)	42 ± 22	23 ± 21	<0.001
Ground vegetation cover (%)	51 ± 22	33 ± 23	<0.001
Litter cover (%)	65 ± 20	71 ± 21	0.138

[a] Two-tailed *t*-tests.
[b] Tree canopy = vegetation >3 cm dbh and >1 m tall.
[c] Shrub layer = vegetation ≤3 cm dbh and >1 m tall.
[d] Ground vegetation = all the plants ≤1 m tall.

The eight Colima Warblers were observed at heights between 0.1 and 6.0 m ($\bar{x}$ = 2.6 ± 2.2 m) in the lush understory in oak-conifer habitat with an average tree canopy height of 16 ± 7 m. Tree canopy cover ($\bar{x}$ = 54 ± 24%), shrub cover ($\bar{x}$ = 53 ± 35%), and ground vegetation cover ($\bar{x}$ = 34 ± 19%) were similar to that found in the breeding season habitat. The three strata in the winter habitat were often contiguous, as they were in the breeding season habitat.

Nine species of birds were common in the lush understory of the oak-conifer woodland and forest where we observed Colima Warblers: White-eared Hummingbird (*Hylocharis leucotis*), House Wren (*Troglodytes aedon*), Russet Nightingale-Thrush (*Catharus occidentalis*), McGillivray's Warbler (*Oporornis tolmiei*), Red Warbler (*Ergaticus ruber*), Golden-browed Warbler (*Basileuterus belli*), Rufous-capped Brush-Finch (*Atlapetes pileatus*), Green-striped Brush-Finch (*A. virenticeps*), and Yellow-eyed Junco. All were observed <1 km from Colima Warblers and on at least three of the four days that we saw Colima Warblers.

Colima Warblers accounted for 2.1% of the 388 wood warblers of 19 species that we observed throughout the oak-conifer woodland and forest; they ranked 13th in abundance. The three most common warblers were Orange-crowned Warblers (*Vermivora ruficapilla*; N = 141), Yellow-rumped Warblers (*Dendroica coronata*; N = 76), and Red Warblers (N = 22).

At least 20 observations (including three specimens) of Colima Warblers

have been recorded in central Mexico between Schaldach's (1963) record and our 1983 observations. There were 19 observations of single birds between September and May in the oak-conifer woodland and forest of central Mexico (1700–3000 m elevation): seven in Distrito Federal, nine in Jalisco, two in Mexico, and one in Michoacan (P. Alden, F. M. Garcia, R. L. Hutto, A. R. Phillips, G. D. Schnell, J. T. Shiflett, and R. H. Wauer, pers. comms.). In addition, Hutto (pers. comm.) observed a Colima Warbler in riparian gallery forest at 640 m elevation in Colima in February 1975.

DISCUSSION

Range and relative abundance.—Our spring field work covered the entire known breeding range of the Colima Warbler. Most of our observations of breeding Colima Warblers were within their previously known distribution. The observations in Zacatecas and San Luis Potosi were apparently new state records. These new sightings were in similar habitat and within 100 km of the warblers' distribution in the adjacent states of Coahuila and Nuevo Leon. There is no evidence that breeding Colima Warblers occur in the oak-pine vegetation south of their known southern limit in Tamaulipas. Colima Warblers have not been found in the Sierra de Guatemala in southern Tamaulipas (Fig. 1), which contains oak chaparral and oak-pine woodland (Robins and Heed 1951, Webster 1974).

Where the Colima Warbler was common during the breeding season, it was often the major representative of the Parulinae. Painted Redstarts (*Myioborus pictus*) occurred in the Colima Warbler habitats where oaks were large and dense. Olive Warblers (*Peucedramus taeniatus*) tended to reside where there were tall pines and other tall conifers. Crescent-chested Warblers (*Vermivora superciliosa*) were common only in the southern half of the Colima Warbler's geographic breeding range and were usually at elevations above most of the Colima Warblers, in cool-moist undergrowth under conifers and quaking aspens (*Populus tremuloides*).

Current observations of the Colima Warbler during the winter season are absent from two recent compendia on nearctic migrants in the Neotropics. Keast and Morton (1980) make no mention of observations of Colima Warblers, not even in the chapter on winter habitat distribution of migratory land birds in western Mexico (Hutto 1980). Rappole et al. (1983) presented only general information on the Colima Warbler, but listed it as most vulnerable in winter and likely to show serious decline within the next decade because of small population size and restricted range (ibid., p. 91). During our communications with observers, we learned of sightings of 20 Colima Warblers in west-central Mexico between 1959 and 1982.

Wintering Colima Warblers were less conspicuous than they were during the breeding season. The paucity of observations of wintering Colima Warblers may be partly explained by their seasonal dispersal from the small breeding range to the larger winter range. We estimated the area of oak and conifer vegetation was 12,000 km^2 in the breeding range and 72,000 km^2 in the winter range. We observed four wintering Colima Warblers per week versus 20 per week in the breeding range, but the oak and conifer vegetation in the winter range covered an area six times larger than the area of similar vegetation in the breeding range.

Breeding habitat.—In Texas, Van Tyne (1936) observed the species frequenting young maples (*Acer grandidentatum*) and deciduous oaks and perching as high as 6 m above the ground. Wauer (1973, 1979) found the species associated with oak–pinyon pine (*P. cembroides*)–juniper and oak–maple–Arizona Cypress environments at elevations between 1700 and 2370 m.

There are only limited descriptions of the Colima Warbler's breeding habitat in Mexico. In southeastern Coahuila, they are a common breeder in chaparral interspersed with pines 4.5 to 6.0 m tall, at elevations from 2180 to 3180 m; in some areas they are common in low encinal (oak-pine woodland; Brown 1982) bordering conifer forest (Ely 1962). Burleigh and Lowery (1942) considered these warblers fairly common above 2270 m on the steep slopes above Diamante Pass in southeastern Coahuila, where singing males have been observed feeding in small oaks. At La Esperanza, Nuevo Leon, Hubbard and Crossin (1974) found Colima Warblers apparently taking nectar from agave (*Agave* sp.) flowers in an area at 2730 m with pines, yuccas (*Yucca* spp.), and scrub oak.

Our observations corroborate and expand these published habitat descriptions. Colima Warblers often foraged and perched in the dense, lower vegetation. Bunchgrass, along with litter, exposed roots, and rocks, provided suitable cover for nests. We observed Colima Warblers and measured features of the habitat in the vicinity of the birds; we did not actively search for the warblers' nests.

We found Colima Warblers in suitable habitat, containing a combination of oak and pine trees, oak shrubs, and bunchgrasses that was present on every mountain of sufficient stature to nourish woodland and forest. The habitat was often on the northern slopes and frequently at the higher elevations of the chaparral and woodland communities and the lower elevations of the pine-conifer forest. Suitable habitat was only in a narrow elevational band in some areas. However, other areas of suitable oak-pine habitat were scattered at various elevations and on diverse exposures of the rugged Sierra Madre Oriental.

Colima Warblers were in undisturbed sites, but they were also found

in areas of light-to-moderate grazing (by domestic animals), selective logging, and burning. Such disturbances to the habitat seemed to be tolerated by the warblers. In some areas, grazing and selective logging seemed to perpetuate the oak chaparral and oak-pine woodland, based on Lanning's (unpubl. data) observations in Coahuila and Nuevo Leon between 1976 and 1986. Colima Warblers were not found in heavily disturbed areas, where the shrubs and ground vegetation under the trees had been destroyed by grazing or recent fires, or in areas that had been cleared for agriculture or dwellings.

Colima Warblers inhabit an area of northeastern Mexico and western Texas that is remote and sparsely populated by humans. Limited areas of oak and conifer vegetation have been cleared for pastures, crops, and dwellings, and some additional areas will undoubtedly be cleared in the future. Most of the habitat occupied by Colima Warblers appears to be too rugged, remote, and unsuitable for agriculture and will only be used for grazing and selective logging. Based on current land-use patterns and the ruggedness of the terrain, there will be suitable habitat in northeastern Mexico and western Texas for breeding Colima Warblers for the foreseeable future.

Winter habitat.—Descriptions of the Colima Warbler's winter habitat is limited to the AOU (1983) general description of woodland, thickets, and scrub and to Schaldach's (1963) specimen from fir forest. Our few observations affirm that Colima Warblers are found in woodland and forest containing oaks, pines, and fir. Further research is needed on what percentage of the available oak and conifer vegetation within the warblers' winter range is used by the Colima Warblers.

We observed wintering Colima Warblers in woodland and forest that had been subjected to limited grazing and selective logging. Several of Mexico's major population centers are in the highlands of central Mexico. Forested areas have been destroyed and replaced by cities and agricultural areas. The extant woodlands and forests near human settlements have been subject to intensive grazing, burning, and logging, whereas more remote montane regions appeared to be less disturbed. The effect of the habitat disturbances and habitat destruction on wintering Colima Warblers needs further study.

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COLOR PLATE

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RED-COCKADED WOODPECKERS VS RAT SNAKES: THE EFFECTIVENESS OF THE RESIN BARRIER

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Abstract.—Red-cockaded Woodpeckers (*Picoides borealis*) excavate resin wells in the immediate vicinity of roost and nest cavity entrances. Resin wells are worked regularly, resulting in a copious and persistent resin flow that coats the tree trunk, especially below cavity entrances. Red-cockaded Woodpeckers also scale loose bark from cavity trees and closely adjacent trees. These two behaviors result in smooth, sticky surfaces surrounding cavity entrances. Climbing experiments on cavity, scaled, and control trees using rat snakes (*Elaphe obsoleta*) demonstrate that these behaviors produce a resinous barrier that is highly effective in preventing predatory snakes from gaining access to active Red-cockaded Woodpecker cavities. *Received 23 Jan. 1989, accepted 15 May 1989.*

Red-cockaded Woodpeckers (*Picoides borealis*) and rat snakes (*Elaphe obsoleta*) are sympatric over an extensive area in the southeastern United States (Jackson 1971, Conant 1985). Unique aspects of the behavioral biology of the Red-cockaded Woodpecker have been hypothesized as adaptations to reduce predation by rat snakes (Dennis 1971a, Ligon 1970). In this paper, we report experimental data supporting the hypothesis that cavity protection behavior, specifically when this behavior results in copious fresh resin accumulation adjacent to cavity entrances, significantly reduces the ability of rat snakes to climb Red-cockaded Woodpecker cavity trees.

The Red-cockaded Woodpecker primarily inhabits mature pine forests over much of the southeastern United States (Jackson 1971) where habitat alteration due to various management procedures has resulted in the species being placed on the Federal list of endangered species (Thompson and Baker 1971, Wood 1983).

Southeastern pine forests, due to climate and the historical importance of fire, provide few dead trees and limbs for cavity construction by woodpeckers (Ligon 1970, 1971). The Red-cockaded Woodpecker, unlike most other woodpecker species, uses living pines as cavity sites, with rare exceptions (Ligon 1970, Patterson and Robertson 1983, Wayne 1910). The selection of living pines, which produce copious resin flows when mechanical damage occurs, places constraints on cavity location and architecture. Cavities need to be located in trunk segments of sufficient diameter

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and age to insure that the occupied chamber is located in the nonliving central heartwood to avoid resin accumulation in the chamber (Beckett 1971; Dennis 1971a, b). Consequently, almost all cavities are located on the bole of the pine, usually below the lowest branches (Ligon 1970). Entrance tunnels, which necessarily pass through living, resin-transporting tissues to reach the nonliving heartwood, are sloped upward. Thus, resin flows are directed toward the exterior of the tree and away from the cavity chamber (Ligon 1970). The excavation of small ancillary holes, termed resin wells, is associated with cavity construction by Red-cockaded Woodpeckers (Ligon 1970, Dennis 1971a). Several resin wells typically are associated with each cavity; these generally are located within a meter above and below the cavity entrance. Resin wells are worked regularly by the birds so that copious resin flow persists (Dennis 1971a, Ligon 1970). An essentially complete coat of fresh resin eventually accumulates on the tree surface surrounding the cavity entrance, often extending several meters below the entrance. In addition, adjacent trees may also have a limited number of resin wells (Dennis 1971a, D. C. Rudolph pers. obs.). Cavity trees and adjacent trees also have loose bark persistently scaled from their boles by Red-cockaded Woodpeckers (Jackson 1978b, Ligon 1970). This behavior results in a reduction of the surface roughness of these trees. Several functions of resin well excavation and bark scaling have been suggested. Lay and Russell (1970) hypothesized a social context for these behaviors, resulting in communication of colony location and/or active status. The majority of hypotheses, however, have involved some aspect of cavity protection, either from predators or potential competitors. Pearson et al. (1942) suggested that resin flows were a "sticky and effective barrier against ants and flying squirrels." Steirly (1957) essentially agreed, and Dennis (1968) suggested defense against avian usurpers. Ligon (1970), Dennis (1971a), and Jackson (1978a) hypothesized that protection from predatory snakes was the primary function.

In this paper we quantify the ability of rat snakes to climb Red-cockaded Woodpecker cavity trees, scaled trees, and control trees to evaluate the effectiveness of the resin barrier.

METHODS

Nine rat snakes (*E. o. lindheimeri*) ranging from 52–180 cm in total length were captured in Nacogdoches County, Texas. Snakes were housed in glass aquaria provided with soil substrate, water, and food. Climbing trials were conducted in active Red-cockaded Woodpecker colonies located in Angelina County, Texas. The primary tree species used for cavity construction by Red-cockaded Woodpeckers in this area is longleaf pine (*Pinus palustris*), and all climbing trials used this species. Experimental trees were chosen based on the following criteria. Cavity trees (N = 3) were selected that exhibited a profuse coating of fresh resin that extended from the cavity to near ground level. Resin was present throughout

the 5-m course and was profuse for 4–4.5 m. Trees that had experienced extensive removal of loose bark by Red-cockaded Woodpeckers, hereafter termed scaled trees (N = 4), were chosen based on extent of bark removal (maximum) and similarity in size to cavity trees. Control trees (N = 4), unaltered by Red-cockaded Woodpecker activity, were chosen based on similarity in size to cavity and scaled trees. The diameters at breast height of all trees were within the range of 47–62 cm.

We established a 5-m climbing course on the trunk of each tree beginning at 1 m above ground level and extending to 6 m above ground level. The course was delineated by short strips of tape applied at 1-m intervals to the bark surfaces. In the case of cavity trees, the course was established on the side of the tree having the most active and copious resin accumulation. Snakes were tested for climbing ability when air temperatures were between 24 and 28°C. Use of molting and recently fed snakes was avoided. Snakes were placed on trunks with their heads positioned at the 1-m mark. The general response was for the snake to grip the bark surface and begin climbing. Most climbed continuously until their heads reached the level of the 6-m tape, when they were removed from the tree. Snakes that stopped climbing for extended periods (>5 sec) were gently prodded near their posterior end using a telescoping fishing pole. This resulted in continued climbing and avoided the influence of long pauses on climbing rates. Snakes that refused to initiate climbing at the 1-m mark, usually by falling or climbing toward the ground, were an occasional problem. Most performed well in subsequent trials. Number of trials per snake varied from 9–11.

Climbing trials were conducted over a period of 60 days after capture of the snakes. To avoid reduced performance due to previous exertion, trials of individual snakes were limited to a maximum of two per day and did not exceed one trial per hour. Trials on cavity trees were limited to one per day per snake to avoid the effects of accumulated resin. A minimum of five days separated trials using cavity trees. For each trial we recorded tree class (cavity, scaled, control), snake total length, and elapsed time of climb. Trials were terminated when snakes fell. In these instances partial distances and elapsed times were recorded.

RESULTS

Preliminary results indicated that climbing rates were influenced by tree diameter. Snakes experienced more difficulty climbing larger diameter trees, presumably due to smoother bark and a greater abundance of easily dislodged bark fragments. This source of variation was substantially reduced in the present study by using only relatively large trees (dbh's of 47–62 cm).

Sixty three trials were conducted on control and scaled trees. In 62 of these trials the snakes successfully completed the 5-m course. No significant difference in climbing success between control and scaled trees was found ($G = 0.52$, $P > 0.05$, df = 1, Yates' correction). In contrast, only three of 18 climbing attempts on cavity trees were successful. Snakes were less likely to climb cavity trees successfully than control and scaled trees combined ($G = 59.44$, $P < 0.001$, df = 1, Yates' correction). The three successful climbs were performed by the two smallest snakes in the sample of nine snakes.

Climbing rates were compared using a repeated measures ANOVA (Table 1). Rate of climbing was the dependent variable; tree class and

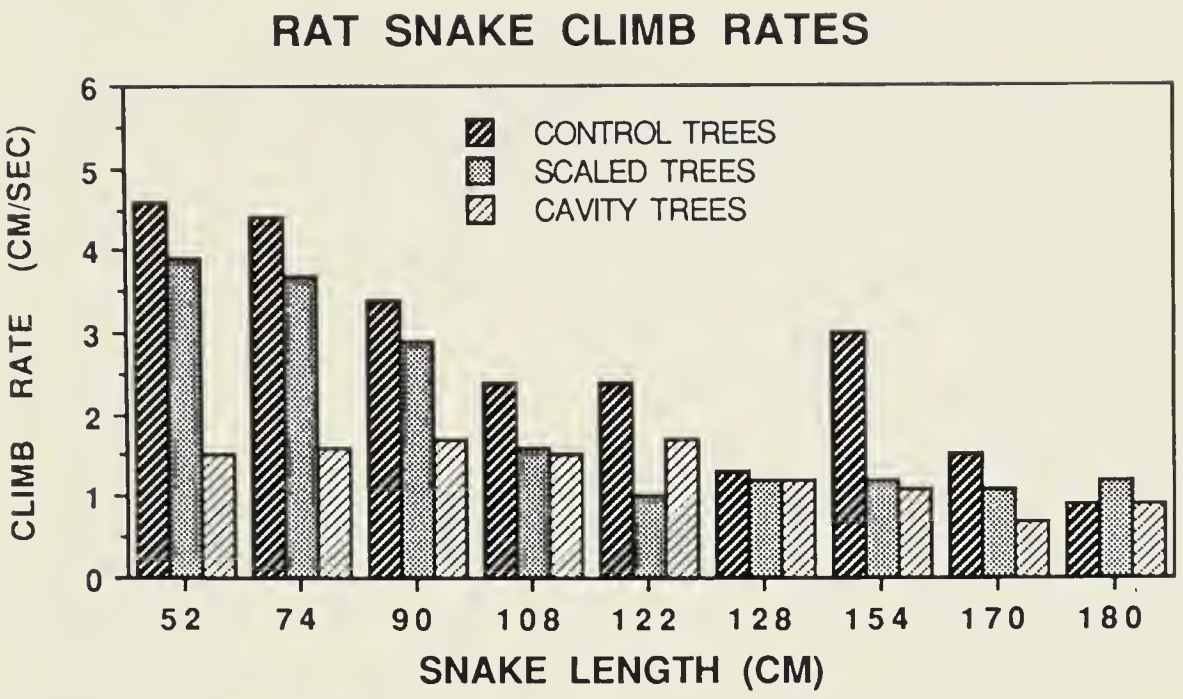

FIG. 1. Climbing rates of rat snakes (*Elaphe obsoleta*) on control, scaled, and cavity trees.

snake total length were the two treatments. The results indicate a significant effect of both treatments (tree class and snake total length) on climbing rate ($P < 0.01$). Larger snakes required progressively more time to complete the experimental climbs, and this pattern was evident across all three tree classes (Fig. 1). The significant effect of tree class resulted from slower climbing rates for scaled trees and cavity trees compared to control trees. Compared to control trees, the smallest individuals experienced relatively little difficulty on scaled trees, but considerable difficulty on cavity trees (see Fig. 1). Larger individuals experienced substantial difficulty on both scaled and cavity trees.

Observation of snakes during the climbing trials provides additional information on several factors contributing to the pattern in climbing rates. Snake size related to climbing ability in two ways. First, the smaller snakes were generally able to insinuate their bodies into crevices between adjacent bark plates and effectively follow these anastomosing crevices up the trunk of the tree. Progressively larger snakes were less able to take advantage of this strategy and relied on a combination of crevices and protruding bark fragments to provide purchase points on the trunks. Searching for suitable paths up the trunk consumed progressively more time with increasing snake size. Second, the larger more massive snakes commonly dislodged loose bark fragments during climbing activity. Thus additional time was required to locate alternate purchase points as well

TABLE 1
ANALYSIS OF THE EFFECT OF TREE CLASS AND SNAKE TOTAL LENGTH ON CLIMBING RATE USING A REPEATED MEASURES ANOVA

Source of variation	Sum of squares	df	Mean square	*F*
Mean	245.81	1	245.53	196.53**
Tree	16.09	2	8.05	6.43*
Snake	58.82	8	7.35	5.88*
Error	18.76	15	1.25	

** $P < 0.001$, * $P < 0.01$.

as often laborious recovery from near falls. These two factors appeared to be the primary contributors to the relationship between climbing rates and snake length.

Tree class had a pronounced effect on climbing behavior. Scaled trees, as compared to control trees, presented fewer purchase points for climbing snakes. As a result, snakes climbing scaled trees progressed with more difficulty and spent more time searching for a suitable route. Cavity trees also lacked rough bark, and in addition resin effectively smoothed over remaining irregularities, presenting the snakes with a relatively smooth surface. Initially snakes attempting to climb cavity trees progressed reasonably well, but as climbs continued the snakes experienced rapidly increasing difficulty. They were unable to maintain purchase points on the trunks over progressively increasing portions of their length, and most eventually fell. Even smaller individuals that successfully completed climbs experienced severe difficulties during the final portions of the climbs.

Examination of snakes immediately after climbing attempts on cavity trees revealed minimum amounts of resin adhering to their ventral surfaces. Small resin patches, a few mm in length, occasionally were noted. However, the overlapping surfaces of the ventral scales commonly had minute amounts of resin adhering to them, and these were often positioned such that they contacted adjacent scales. The result was a loss of mobility of the ventral scales important in this type of climbing.

Immediately after unsuccessful climbing trials on cavity trees, several snakes were observed on the ground. Their progress and behavior appeared normal. These individuals were also placed on control trees and their climbing efforts observed. They were unable to climb, or experienced considerable difficulty. Their behavior closely resembled that exhibited during climbs on resin-coated cavity trees. Residual resin reducing scale mobility was the probable cause of this climbing difficulty.

DISCUSSION

The rat snake is a common semiarboreal species found throughout the range of the Red-cockaded Woodpecker, with numerous recognized subspecies (Conant 1985).

The climbing abilities of *E. obsoleta* are well known (Curran and Kauffeld 1937, Wright and Wright 1957). Prey composition data indicate that birds and their eggs comprise a significant percentage of the diet of *E. obsoleta,* at least during avian breeding periods (Fitch 1963, Hensley and Smith 1986). Dennis (1971a) and Jackson (1978a) document four instances of *E. obsoleta* gaining access to Red-cockaded Woodpecker cavities. Two involved empty cavities, one cavity was occupied by flying squirrels (*Glaucomys volans*), and one cavity contained nestling Red-cockaded Woodpeckers. However rat snakes have difficulties in traversing the resin-coated surfaces (Dennis 1971a, Jackson 1978a, Summerour 1988). All observations of rat snakes successfully gaining access to cavities involve cavities whose resin barrier was compromised.

Jackson (1974) simulated resin-coated pine trunks in a laboratory setting and quantified rat snake climbing frequencies. A 2-cm band of fresh resin did not reduce climbing frequency; the snakes easily were able to arch their bodies over the resin band. The coating of extensive portions of the trunk with resin drastically reduced climbing frequencies compared to controls. Climbing frequency was also monitored during a subsequent 24-day period as the fresh resin dried. A significant increase in climbing frequency occurred with progressive drying of the resin.

In Jackson's (1974) experimental protocol, snakes that climbed resin-coated trunks experienced significant resin accumulation on their bodies. Abnormal behavior consisting of writhing and holding the body in stiff loops resulted. One individual subsequently died, possibly as a result of toxic effects of the resin. Jackson concluded that the snakes were affected by the stickiness of the resin, which cemented some of the scales together, and possibly by the potentially toxic effects of resin constituents, especially phenols.

The results presented support the hypothesis that resin wells and the resulting resin coating adjacent to Red-cockaded Woodpecker nest and roost cavities reduces access to these cavities by *E. obsoleta,* potentially the most significant snake predator of cavity-nesting birds in the southeast United States. The effectiveness of the resin barrier is indicated by the low incidence of climbing success (3/18 attempts) exhibited by snakes in the experiment. In an actual predation attempt, snakes would be required to negotiate the final distance to the cavity entrance, an additional 1–2 m in the case of the experimental trees, which the experimental climbing

course did not include. This area typically contains the heaviest and freshest resin accumulations. Consequently, cavity protection should be even more effective than these data indicate.

The scaling of loose bark from trees adjacent to cavity trees had no effect on rat snake climbing success. The reduced roughness of the trunk did, however, reduce the climbing rate of the snakes. Extensive scaling of loose bark from the cavity tree results in a smoother trunk and more even coverage by flowing resin. In this context the bark scaling behavior of Red-cockaded Woodpeckers undoubtedly increases the effectiveness of the resin barrier.

Jackson (1974) suggested that both the physical stickiness of the resin and potential toxic effects of resin deterred rat snakes. Jackson's experimental protocol resulted in copious amounts of resin adhering to the experimental snakes. In contrast, the protocol followed in our experiments, which closely resemble the actual situation faced by predatory snakes in the field, resulted in minimal amounts of resin accumulating on the ventral surfaces of the snakes. However, the mechanical effects of small amounts of resin picked up by the overlapping surfaces of individual scales, resulting in a tendency of adjacent scales to adhere, reduced the mobility of the ventral scales, and resulted in inability to climb. The limited direct contact with resin and the time involved in climbing reduces the probability of toxic effects of resin constituents. However, the potential repellent/toxic properties of resin constituents under natural conditions need to be tested further.

Elaphe obsoleta is an abundant and efficient predator on nesting birds in southeastern United States pine forests. Although data on actual predation rates are not available, anecdotal evidence suggests that it is a significant factor confronting many species of birds, including Red-cockaded Woodpeckers. Red-cockaded Woodpeckers exhibit an elaborate behavioral repertoire that produces a resin barrier effective in reducing access of rat snakes to their roost and nest cavities. J. R. Walters (in press) and J. A. Jackson (pers. comm.) indicate that Red-cockaded Woodpeckers have an extremely low nest predation rate compared to other cavity-nesting species. We support the hypothesis that reduction of snake predation, primarily by those in the genus *Elaphe,* is a major selective factor in the evolution of the behaviors of Red-cockaded Woodpeckers that result in the maintenance of resin coatings on cavity trees. Additional data quantifying actual snake predation rates on nesting birds in southeastern pine forests and the effectiveness of resin barriers in actually reducing snake predation would provide further insight.

The alternative hypotheses that have been proposed as selective factors culminating in the production of resin coating on Red-cockaded Wood-

pecker cavity trees are not mutually exclusive. Hypotheses proposed concern three general types of selective benefits; communication functions (Lay and Russell 1970), reduction of non-snake predation (Pearson et al. 1942, Ligon 1970, Dennis 1971a), and reduction of competition for cavities by other species (Ligon 1970, Dennis 1971b). Specific evaluation of these alternative hypotheses is necessary to determine if they are significant factors in the evolution of Red-cockaded Woodpecker behavior related to resin well construction on cavity trees.

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COMPETITION FOR RED-COCKADED WOODPECKER ROOST AND NEST CAVITIES: EFFECTS OF RESIN AGE AND ENTRANCE DIAMETER

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Abstract.—Competition for roost and nest cavities was investigated in a Texas population of Red-cockaded Woodpeckers (*Picoides borealis*) in longleaf pine (*Pinus palustris*) habitat. Twenty-two percent of all examined cavities were occupied by Red-cockaded Woodpeckers, and 46% were occupied by other species. Red-cockaded Woodpeckers did not roost in the open or in sub-optimum cavities due to the presence of other species, with one temporary exception. Southern flying squirrels (*Glaucomys volans*) were a potential competitor. Similar to Red-cockaded Woodpeckers, flying squirrels preferred cavities with small entrance diameters, and their use of cavities was not hampered by the presence of a resin barrier or woodpecker cluster status (active vs inactive). Other potentially competing species were either rare or restricted to enlarged cavities no longer used by Red-cockaded Woodpeckers. These data suggest that competition for cavities is not an important factor in this particular population of Texas Red-cockaded Woodpeckers during the period prior to breeding. *Received 3 Nov. 1988, accepted 1 May 1989.*

The Red-cockaded Woodpecker (*Picoides borealis*) inhabits mature pine forests in the southeastern United States. Red-cockaded Woodpecker population structure is complex, consisting of parent-offspring groups termed clans (Ligon 1970). A Red-cockaded Woodpecker clan typically consists of a breeding pair and some male offspring of previous years (Ligon 1970, Gowaty and Lennartz 1985). Non-breeding male clan members, called helpers, assist the breeding pair in maintaining cavities, feeding young, and other activities (Baker 1971, Ligon 1970, Lennartz and Harlow 1979). Female offspring disperse prior to the breeding season following fledging (Gowaty and Lennartz 1985, J. A. Jackson pers. comm.). Clans occupy clusters consisting of one to many cavity trees that provide roosting and nesting sites (Ligon 1970, 1971; Hooper and Lennartz 1983).

Due to climate and the historical importance of fire, southeastern pine forests provide minimal numbers of dead trees and limbs for cavity construction by woodpeckers (Ligon 1970, 1971). But Red-cockaded Woodpeckers are unique among woodpeckers in their nearly exclusive use of living pines for cavity sites (Ligon 1970, Short 1979). Red-cockaded Woodpecker cavities are typically excavated in the trunks of pines, often below the lowest branches (Ligon 1970, Wood 1983). Entrance tunnels that pass through living, resin-transporting tissue, slope upward to the

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interior, which directs resin flow toward the exterior and away from the cavity chamber (Dennis 1971a, Jackson 1978a).

Red-cockaded Woodpeckers also construct small ancillary holes, termed resin wells, in the immediate vicinity of the cavity entrance (Steirly 1957, Ligon 1970, Dennis 1971a). Because these resin wells are worked regularly by the birds, resin flow persists. The eventual result is a copious coating of resin around the cavity entrance and several meters below. In addition, the woodpeckers persistently scale loose bark from the trunk of the cavity tree resulting in a smoother surface and a more even and complete resin coating (Ligon 1970, Dennis 1971a, Jackson 1978b).

Several hypotheses have been suggested to explain the evolution of Red-cockaded Woodpecker behavior involving this scaling of bark and the constructing and maintaining of resin wells. Lay and Russell (1970) proposed a social context for these behaviors, suggesting that the changed appearance of the trunks of cavity trees might advertise the birds' location and status. Reduction of predation, especially by snakes, has been hypothesized by Pearson et al. (1942), Dennis (1971a), and Ligon (1970).

Ligon (1970) and Dennis (1971a) have also proposed that the smooth resin-coated trunks reduce interspecific competition for cavities. Definitions and theoretical formulations of interspecific competition require that population size be negatively affected by the interaction. In practice, detrimental effects of potential competitors on survival or reproduction are considered evidence of competitive interaction. In the case of Red-cockaded Woodpeckers, cavity use by other species would not necessarily represent competition. However, if Red-cockaded Woodpeckers were roosting in the open due to other species occupying suitable cavities, then detrimental effects due to competition could be inferred. More subtle effects of competition, due to attempted cavity usurpation and cavity enlargement, resulting in increased energy demands for defense and construction of additional cavities, might also occur.

Testing and evaluation of these hypotheses, which are not mutually exclusive, has been minimal. Jackson (1974) and Rudolph et al. (1990) have presented data demonstrating the effectiveness of resin in preventing access to Red-cockaded Woodpecker cavities by rat snakes (*Elaphe* spp.). Baker (1971), Dennis (1971a), Harlow and Lennartz (1983), Hopkins and Lynn (1971), and Jackson (1978a) have documented extensive use of Red-cockaded Woodpecker cavities by other species. Previous studies have not, however, examined the use of cavities by species other than Red-cockaded Woodpeckers in relation to the cavity requirements of the Red-cockaded Woodpeckers and the status of the potential resin barrier.

This paper presents data specifically collected to evaluate the impact of potential cavity competitors on Red-cockaded Woodpeckers. Complete

cavity surveys were conducted in active and inactive clusters. Data were obtained on cavity use by Red-cockaded Woodpeckers and other species, cavity availability, and status of the resin barrier. The resulting data base was used to examine specific questions relating to cavity use by Red-cockaded Woodpeckers and potentially competing species.

STUDY AREA AND METHODS

This study included all known Red-cockaded Woodpecker clusters in the portion of the Angelina National Forest located south and west of Lake Sam Rayburn, Angelina and San Augustine counties, Texas. The population contained 16 currently active clusters, and 30–50 individuals, during our study. The population has been declining during the past 20 years (D. W. Lay pers. comm.). Vegetation here is a pine-hardwood mosaic with longleaf pine (*Pinus palustris*) dominating the uplands occupied by Red-cockaded Woodpeckers. The area is managed for timber production with longleaf pine typically managed on an 80-year rotation. Red-cockaded Woodpecker cluster sites are managed as separate stands. Prescribed burning has been conducted at irregular intervals. Locke et al. (1983) provide detailed information about the study area and cavity-tree characteristics.

Red-cockaded Woodpecker cavities were surveyed diurnally in active and inactive clusters between 19 March and 22 May 1986. Surveys in active clusters were completed by 25 April, prior to the initiation of egg laying by the Red-cockaded Woodpeckers. Sectional climbing ladders were used to climb cavity trees. Mirrors and a headlamp were used to determine cavity contents. All cavities located in trees exhibiting signs of current Red-cockaded Woodpecker use were surveyed. Cavities in inactive trees were omitted occasionally due to excessive height or obstructing limbs.

The interiors of all cavities, including occasional vertical extensions above the cavity entrance (Beckett 1971), were examined visually. All vertebrate species and active wasp nests were recorded. Nest material was noted and a brief description recorded. In active Red-cockaded Woodpecker clusters, the number of clan members and their roost sites were determined. Visual observations were conducted in the morning and evening as the birds exited and entered their roost cavities. Strategic positioning of 1–2 observers allowed the roost sites of all clan members to be determined in 1–5 observation periods per cluster.

Cavity entrance diameter was measured at the point of narrowest constriction using a drafting compass and rule. A 5-category classification of resin age was established, and the resin surrounding each cavity was assigned to the appropriate category. The categories and definitions were: (1) very fresh—copious amounts of clear, semi-fluid, actively flowing resin, (2) fresh—resin solidified and yellowed, but sticky to touch, (3) old—resin dried, not sticky to touch, (4) very old—resin very dry, large areas free of resin due to growth of tree and progressive loss of bark, and (5) absent—most resin lost due to continued growth of tree. These categories are clearly subjective to some extent, but in this study were sufficient to characterize the basic pattern of resin age.

RESULTS

A total of 123 cavities in 89 trees (87 *P. palustris*, 2 *P. taeda*) were examined. The 89 trees comprised 16 active and 15 inactive clusters, plus six isolated inactive trees that were not associated with a specific cluster. Diurnally active tree squirrels (*Sciurus* spp.) were potentially absent from cavities at the times of individual surveys. Cavities known to be used by

TABLE 1
CAVITY CONTENTS IN ACTIVE AND INACTIVE RED-COCKADED WOODPECKER CLUSTERS

Contents		Active clusters	Inactive clusters
Red-cockaded Woodpecker	*Picoides borealis*	27	0
Southern flying squirrel	*Glaucomys volans*	15	12
Tree squirrels	*Sciurus* spp.	8	4
Eastern Screech-Owl	*Otus asio*	2	3
Great Crested Flycatcher	*Myiarchus crinitus*	1	2
Tufted Titmouse	*Parus bicolor*	0	3
American Kestrel	*Falco sparverius*	0	1
Evening bat	*Nycticeius humeralis*	0	1
	Wasps (3 spp.)	2	2
	Water	0	1
	Empty	25	14
	Total	80	43

tree squirrels contained abundant pine needles, typically filling the entire cavity. Cavities containing typical tree squirrel nests were recorded as being occupied by tree squirrels even if squirrels were not observed. Seven of 12 tree squirrel records (Table 1) refer to nests only. Avian records in Table 1 all consist of active nests. Breeding activity of cavity-nesting birds exhibits an April–May maximum in east Texas (pers. obs.). Thus the one-time survey does not cover yearlong cavity use by nesting birds but should approximate the maximum possible at any one time. Roosting in cavities by avian species other than Red-cockaded Woodpeckers was not observed during morning and evening observation periods and apparently was minimal.

A total of 83 (68%) cavities were occupied, and one other cavity contained water. Eight vertebrate species and three wasp species were recorded in cavities in addition to Red-cockaded Woodpeckers. A ninth vertebrate species, the Wood Duck (*Aix sponsa*), nested in a cavity subsequent to the initial survey. Red-cockaded Woodpeckers roosted in 22% of the available cavities. Flying squirrels and tree squirrels were the most frequent of the remaining species (22% and 10%, respectively). All other species occupied a total of 14% of all available cavities. No significant difference was indicated between occupancy rates of all species in active and inactive clusters (G-test, $P > 0.05$).

Red-cockaded Woodpeckers occupied cavities ranging from 40–58 mm in entrance diameter (Table 2). Of the nine other vertebrate species recorded, five (fox squirrel [*S. niger*], eastern gray squirrel [*S. carolinensis*],

TABLE 2
RANGES OF CAVITY ENTRANCE DIAMETERS (MM) OF CAVITIES OCCUPIED BY VERTEBRATE SPECIES

Species		Cavity entrance diameter		Sample size
		Mean	(Range)	
Red-cockaded Woodpecker	*Picoides borealis*	49	(40–58)	27
Southern flying squirrel	*Glaucomys volans*	66	(41–89)	27
Tree squirrels	*Sciurus* spp.	93	(73–115)	12
Eastern Screech-owl	*Otus asio*	96	(72–125)	5
American Kestrel	*Falco sparverius*	90	(90)	1
Wood Duck	*Aix sponsa*	108	(108)	1
Tufted Titmouse	*Parus bicolor*	61	(56–71)	3
Great Crested Flycatcher	*Myiarchus crinitus*	70	(46–85)	3
Evening bat	*Nycticeius humeralis*	51	(51)	1

Eastern Screech-Owl [*Otus asio*], American Kestrel [*Falco sparverius*], and Wood Duck) were restricted to cavities with larger entrance diameters (72–125 mm) than those occupied by Red-cockaded Woodpeckers. Three uncommonly occurring species (Tufted Titmouse [*Parus bicolor*], Great Crested Flycatcher [*Myiarchus crinitus*], and evening bat [*Nycticeius humeralis*]) occupied cavities with entrance diameters (51–85 mm) overlapping the range of diameters of cavities occupied by Red-cockaded Woodpeckers. The remaining species, flying squirrels, used cavities with a range of entrance diameters (41–89 mm) that completely overlapped the entrance diameter range of cavities used by Red-cockaded Woodpeckers.

Red-cockaded Woodpeckers used a restricted range of available cavities in relation to entrance diameter and resin age (Fig. 1). The 27 Red-cockaded Woodpeckers observed roosted in cavities of the two smallest entrance diameter classes and the two freshest resin age categories, with two exceptions. The two exceptions were birds roosting in cavities with old resin (category 3). One was a single bird reoccupying an abandoned cluster site; four weeks later resin wells were active and the cavity would have been classified in category 1. The second was a bird in a large cluster with available category 1 and 2 cavities. Ten days after the survey, this bird was roosting in one of these cavities and was present there four weeks later. Cavities of the two smallest entrance diameter classes and the two freshest resin age classes are hereafter termed "optimal" Red-cockaded Woodpecker cavities.

Thirty-five optimal Red-cockaded Woodpecker cavities were recorded

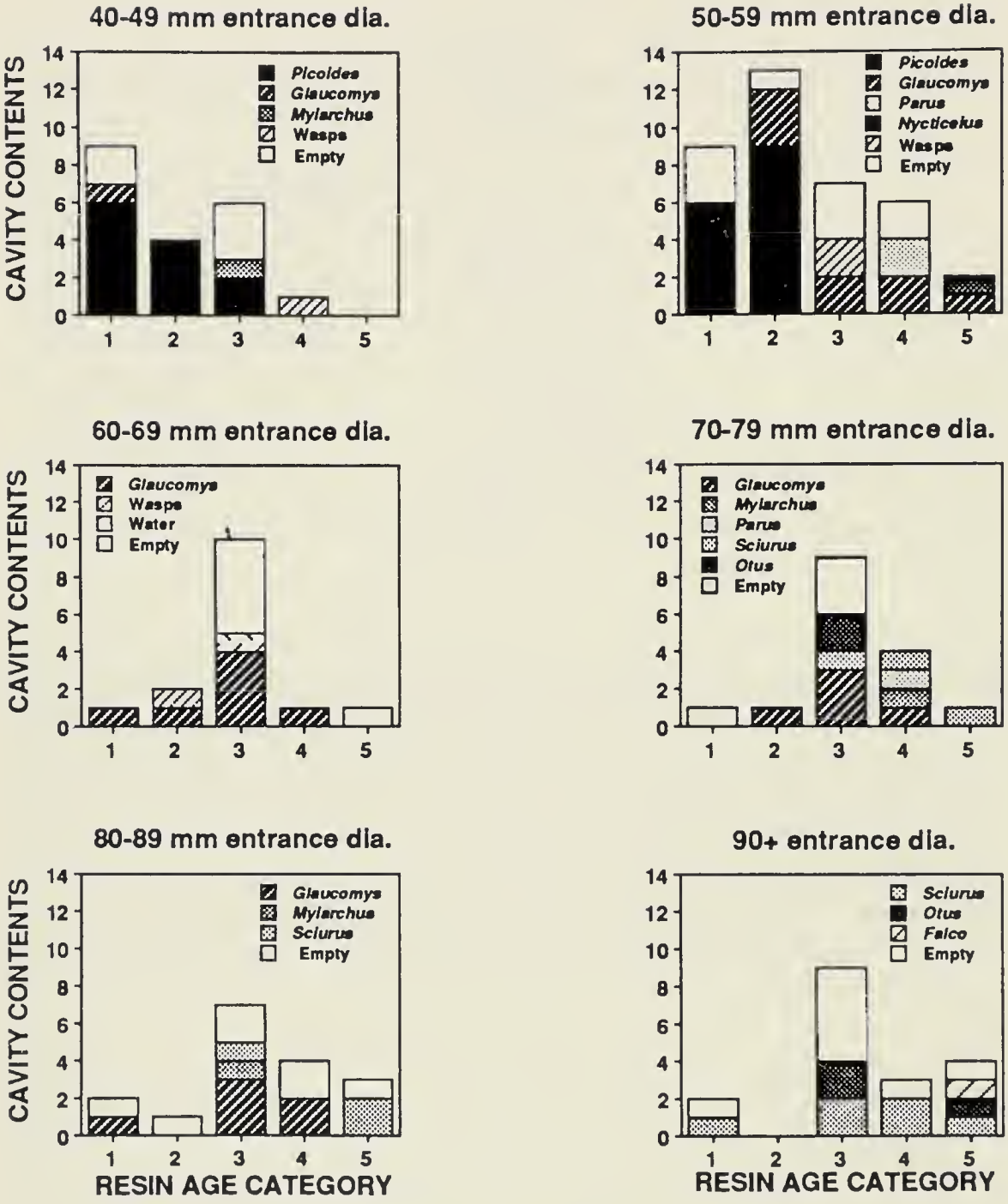

FIG. 1. Cavity contents in relation to entrance diameter and resin age category.

in 16 active clusters. Twenty-five of these cavities were used by Red-cockaded Woodpeckers as roost cavities at the time of the survey. In five clusters, the number of optimal cavities equaled the number of birds present in the clan. Nine clusters contained optimal cavities in excess of the number of clan members (eight clusters with one excess cavity, one cluster with two excess cavities). The two remaining clusters contained one and two fewer optimal cavities than clan members. These two clusters

lacked non-optimal cavities and the three additional birds roosted in the open in the crowns of cavity trees. The ten additional optimal cavities were empty (6) or occupied by flying squirrels (4). In no instance during the survey was a Red-cockaded Woodpecker roosting in the open, or in a non-optimal cavity, due to the presence of other species in optimal cavities.

However, some additional observations are pertinent. After the cavity survey, an optimal cavity previously used as a roost site by a Red-cockaded Woodpecker, was occupied by a flying squirrel. This particular cluster contained three optimal cavities and one old cavity showing no recent activity. The clan was comprised of three birds that had previously used the three optimal cavities as roost sites. The flying squirrel occupied the optimal cavity for at least one week. During this period, evening roosting behavior of the Red-cockaded Woodpeckers was observed three times. In each instance, one of the Red-cockaded Woodpeckers approached the cavity entrance at the normal roost time, peered in once or twice, and flew to an adjacent tree. No direct interaction between the flying squirrel within the cavity and the Red-cockaded Woodpecker was observed. On each occasion, the Red-cockaded Woodpecker eventually roosted in the crown of an adjacent cavity tree. One week later, the flying squirrel was absent, and a Red-cockaded Woodpecker was roosting in the cavity again.

Following the initial cavity survey, a number of cavities previously occupied by either Red-cockaded Woodpeckers or flying squirrels were resurveyed. These observations were made at various times 7–31 days after the original survey. Twenty-one cavities used as roosts by Red-cockaded Woodpeckers during the initial survey were resurveyed. Nineteen were still occupied by woodpeckers, one contained the flying squirrels discussed above and was subsequently re-occupied by the Red-cockaded Woodpecker, and one was a sub-optimum cavity abandoned in favor of an optimum cavity. Fifteen cavities occupied by flying squirrels during the initial survey were resurveyed. Six were still occupied by flying squirrels and nine were empty.

Flying squirrels occupied a wide range of cavities in relation to resin age and entrance diameter (Fig. 1). Cavities ranging in entrance diameter from essentially the smallest available up to 89 mm and of all resin age categories were used. To provide a more detailed understanding of flying squirrels' cavity use, it is necessary to compare cavity use with availability. Accepting the argument that Red-cockaded Woodpeckers can maintain possession of cavities against the challenge of potential flying squirrel competition, and assuming that at least some of the remaining species, especially the larger ones, do also, the best measure of cavity availability for flying squirrels is the number of empty cavities. Observation of flying

squirrels displaced from cavities confirms that they have detailed knowledge of the location of additional cavities within their activity ranges (Sawyer and Rose 1985, pers. obs.).

The number of cavities occupied by flying squirrels was compared to the number of empty cavities in relation to three factors: cluster status, resin age, and cavity entrance diameter. In active clusters 15 of 40 cavities were occupied vs 12 of 26 in inactive clusters. A *G*-test indicated no significant difference ($G = 0.109$, $P > 0.05$). A comparison of flying squirrel occupancy vs resin age revealed eight of 18 cavities of resin age categories 1 or 2 occupied compared to 19 of 48 cavities of resin age categories 3, 4, and 5. No significant difference was indicated ($G = 0.385$, $P > 0.05$). A comparison of flying squirrel occupancy vs cavity entrance diameter revealed 27 of 58 cavities with entrance diameters <90 mm occupied vs 0 of 8 with entrance diameters >90 mm. This difference was highly significant ($G = 15.597$, $P < 0.01$). Due to small sample sizes, Yates' correction was used in all tests.

The remaining species comprise the group (tree squirrels, Eastern Screech-Owl, American Kestrel, Wood Duck) restricted to cavities with entrance diameters larger than those typically occupied by Red-cockaded Woodpeckers. This diverse assemblage undoubtedly responded to cavity characteristics in various ways. Sample sizes are too small to conclude much beyond the obvious limitations of entrance diameters. This is especially true because cavities with larger entrance diameters and fresher resin are rare. Two observations are worth noting, however. A fox squirrel and a Wood Duck were each able to raise young in a cavity with extremely fresh, copious resin. This was actually the same cavity used sequentially, and was also in the tree that contained the current nest cavity of the Red-cockaded Woodpeckers. Neither species exhibited any obvious difficulty with the resin.

The smaller species (Tufted Titmouse, Great Crested Flycatcher, evening bat, wasps) used cavities of smaller entrance diameters, but, except for one cavity occupied by wasps, were restricted to cavities with resin of the three older age categories. However, the sample size is small and not too much should be made of this. The literature suggests that various small and medium-sized avian species are able to use cavities with fresh, well-developed resin barriers (Jackson 1978a, Harlow and Lennartz 1983, Ligon 1971).

DISCUSSION

Surveys and incidental observations have identified more than 20 species of birds and mammals using Red-cockaded Woodpecker cavities as roost and/or nest sites (Baker 1971, Dennis 1971a, Harlow and Lennartz 1983,

Hopkins and Lynn 1971, Jackson 1978a, this study). Reported occupancy rates for vertebrate species other than Red-cockaded Woodpeckers are 35% (Dennis 1971a), 46% (this study), and 56% (Harlow and Lennartz 1983) of available cavities. The potential for significant competition for cavities between Red-cockaded Woodpeckers and other species therefore exists. Determining if competition actually occurs is difficult. Many of the occupied cavities are presumably unsuitable for Red-cockaded Woodpeckers. Also, quantitative data are usually lacking on the cavity requirements of individual Red-cockaded Woodpecker clans and the availability of cavities in the clusters. Dennis (1971a), however, comments that many woodpecker cavities occupied by other species are enlarged and/or long abandoned.

A number of possible instances of competition involving cavities have been documented. Ligon (1971) observed a Red-bellied Woodpecker (*Melanerpes carolinus*) physically removing a Red-cockaded Woodpecker from a cavity, and found cavity defense against Red-bellied Woodpeckers an important part of Red-cockaded Woodpecker behavior. Baker (1971) reported sequential use of a cavity by Red-bellied Woodpeckers and Red-cockaded Woodpeckers. Jackson (1978a) reported the abandonment of two Red-cockaded Woodpecker colonies presumably due to the usurping of all active cavities by Red-bellied Woodpeckers. Harlow and Lennartz (1983) reported the failure of two clans to breed during four of twelve years due to the occupancy of potential nest cavities by Eastern Bluebirds (*Sialia sialis*) and flying squirrels.

Cavity characteristics and differences among species in types of cavities used must be considered to evaluate cavity use in the woodpecker clusters. Cavities constructed by Red-cockaded Woodpeckers are suitable as roost and nest cavities at the time of completion. These cavities are characterized by small entrance diameters and active resin wells. Cavities may remain suitable for use by Red-cockaded Woodpeckers for many years (Lay and Russell 1971, Jackson 1978a). Over a period of years, barring death of the tree, cavities evolve into having larger entrance diameters and inactive resin wells. Cavity entrance enlargement by other woodpeckers, squirrels, and fire (Beckett 1971, Jackson 1978a, Conner and Locke 1979) eventually results in a cavity unsuitable for Red-cockaded Woodpeckers. Enlargement may occur before or after abandonment of a cavity by Red-cockaded Woodpeckers. After abandonment by Red-cockaded Woodpeckers, resin flow declines to a very low level, and progressive drying and loss of the once well-developed resin coating occurs. Inactive cavities with inactive resin wells can be reactivated by Red-cockaded Woodpeckers if entrance diameters are still acceptable.

The data reported here quantified the cavity requirements of individual

Red-cockaded Woodpecker clans and the availability of cavities in the respective clusters. In no instance, during the initial survey, was a Red-cockaded Woodpecker roosting in the open, or in a sub-optimal cavity, due to the occupancy of cavities by other species. Red-cockaded Woodpeckers roosting in the open (N = 3) or in sub-optimal cavities (N = 2) were in clusters with insufficient cavities, except for the bird in a sub-optimum cavity from which it later moved to an optimal cavity. The observation of a flying squirrel temporarily displacing a Red-cockaded Woodpecker to an open roost site was the only example in this study of cavity loss due to another species. Thus, competition for available roost cavities appears minimal during the period prior to the breeding season in this Red-cockaded Woodpecker population.

Five of the species using Red-cockaded Woodpecker cavities were restricted to cavities with entrance diameters larger than those used by Red-cockaded Woodpeckers. These species and others reported in the literature (Dennis 1971a) are substantially larger than Red-cockaded Woodpeckers and cannot use optimal Red-cockaded Woodpecker cavities. Interactions between these species and Red-cockaded Woodpeckers occur in the context of the historical aspects of cavity enlargement. In this population, cavity enlargement by Pileated Woodpeckers (*Dryocopus pileatus*) is common. These interactions may be important but have not been examined.

The remaining species are smaller and can use optimal Red-cockaded Woodpecker cavities. Flying squirrels are the most abundant of these species. The data from this study support two general conclusions relevant to competition between these two species. First, flying squirrels are not displacing Red-cockaded Woodpeckers from optimal cavities in this population during the period prior to the breeding season. This conclusion is supported by the lack of examples of displacement (see below for a discussion of the one exception) and the lower flying squirrel occupancy rate of optimal cavities compared to non-optimal cavities. Second, flying squirrels are not prevented from using cavities protected by a copious and fresh resin barrier. No significant difference was found in flying squirrel occupancy rates of cavities with fresher resin (categories 1 and 2) compared to those with older resin (categories 3 to 5). Observations of flying squirrels occupying cavities with a fresh resin barrier indicated no obvious difficulty with the resin accumulations. Beckett (in Dennis 1971a) reported only small amounts of resin on the feet of flying squirrels occupying similar cavities.

The observation of a Red-cockaded Woodpecker roosting in the open while its previous roost cavity was occupied by a flying squirrel is of interest. The Red-cockaded Woodpecker maintained an interest in the cavity at roost time, but made no direct attempt to displace the squirrel.

The bird subsequently re-occupied the cavity. This is the only published account of interaction between these two species other than data on sequential cavity occupation. How is this observation to be reconciled with the pattern of cavity occupation indicating that flying squirrels are not displacing Red-cockaded Woodpeckers from optimal cavities?

We hypothesize that both Red-cockaded Woodpeckers and flying squirrels may be unable to evict the other species when the other species is already in a cavity. Red-cockaded Woodpeckers are diurnal (roost times in Baker 1971) and flying squirrels are nocturnal (Sonenshine and Levy 1981), and their normal activity periods do not overlap. Consequently, either species searching for a cavity at the conclusion of its normal activity period would probably encounter the other species already occupying cavities in presumably invincible positions. If, as the limited data reported above suggest, Red-cockaded Woodpeckers are consistent in their use of a specific cavity, and flying squirrels much less so, the observed pattern of cavity occupancy would rapidly develop. Red-cockaded Woodpeckers would relatively quickly encounter the optimal cavities vacant, and once occupied, they would hold them for extended periods. This obviously begs the question of how the flying squirrel referred to above obtained the Red-cockaded Woodpecker's roost cavity, but exceptions always occur. Also, if the cluster areas contain a lower ratio of optimal to suboptimal cavities, the level of competition might be increased because of reduced availability of diurnal roosting sites for flying squirrels.

The data reported support the conclusion that interspecific competition for cavities is minimal in this Red-cockaded Woodpecker population prior to the breeding season. Competition may vary temporarily, and the existence of significant competition at other times should not be discounted. In particular, the limited availability of excess cavities may result in intense competition at the time of woodpecker fledging when cavity requirements of clans increase. In addition, the potential exists for predation by flying squirrels on eggs and nestlings and other detrimental interactions. Data are currently lacking on these aspects of the flying squirrel-Red-cockaded Woodpecker interaction.

Variation in population levels of competitors, especially flying squirrels, could also alter the level of competition for cavities. Other studies, in particular Harlow and Lennartz (1983), Jackson (1978a), and Ligon (1971) suggest the possibility of significant competition from other woodpeckers, especially Red-bellied Woodpeckers. Cavity usurpation, ejection of Red-cockaded Woodpecker nestlings, and frequent agonistic encounters were reported. Two considerations may be involved in the apparent discrepancies between these studies and the present study. First, methods and sample sizes differ. The cited studies examined more clusters and also

included extensive observations of behavior. The instances of interaction were thus obtained from a larger pool of possibilities. Second, the level of competition and other interactions may vary with location. Although Red-bellied Woodpeckers were moderately common at our study site, ample lightning and beetle-killed pines appeared to be available for the Red-bellied Woodpecker population. We also suspect that competition with Red-bellied Woodpeckers would be higher in habitats with more hardwoods. Thus, the availability of alternatives may be a major influence on the extent of competition for cavities between species of woodpeckers.

There is no evidence that the resin barrier significantly reduced competition for cavities. Red-cockaded Woodpeckers apparently have no specific behavioral adaptations to avoid problems with resin, so it is not unexpected that other vertebrate species, at least those with limbs, have little difficulty occupying resin-protected cavities.

Five instances of birds entrapped in the resin of Red-cockaded Woodpecker cavities have been reported. These examples, two Red-cockaded Woodpeckers (Locke et al. 1979, pers. obs.), a Red-bellied Woodpecker (Barnett et al. 1983), a bluebird (Dennis 1971a), and a warbler (Dennis 1971b) possibly represent mortality directly attributable to the resin barrier. Despite these examples, cavity-nesting species can successfully use Red-cockaded Woodpecker cavities with well-developed resin barriers, and the benefits of a cavity protected from predatory snakes may more than compensate for some resin-induced mortality. Additional data comparing occupancy rates of cavities with fresh resin to those with older resin, similar to the data reported here for flying squirrels, would be informative.

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WILSON ORNITHOLOGICAL SOCIETY–ASSOCIATION OF FIELD ORNITHOLOGISTS JOINT ANNUAL MEETING

The Wilson Ornithological Society and the Association of Field Ornithologists will hold a joint meeting 31 May–3 June 1990, at Wheaton College, Norton, Massachusetts. Featured parts of the program include symposia on "The Amateur in Ornithology" (including Mary Clench, Harold Mayfield, John Tautin, and Robert Yunick) and "North American Avian Zoogeography" (Chandler Robbins, Russell Greenberg, Elliot Tramer, and Francois Vuillemier). Keith Bildstein will lead a workshop on conservation of coastal wetlands in the western hemisphere and Chris Rimmer will lead one on how to set up a long-term study. For further information contact:

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REPRODUCTIVE SUCCESS AND NESTING HABITAT OF LOGGERHEAD SHRIKES IN NORTH-CENTRAL SOUTH CAROLINA

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ABSTRACT.—Breeding Loggerhead Shrikes (*Lanius ludovicianus*) were studied in the Piedmont physiographic region of north-central South Carolina during the breeding seasons of 1986 and 1987. Sixty-three percent of shrike nests were in red cedar (*Juniperus virginiana*). Shrikes nesting in red cedar fledged one more young per nest than did shrikes nesting in other trees. First nests were significantly lower and somewhat closer to the trunk of the nest tree than were second nests, suggesting that climatic effects during the nesting season affected nest placement. Within 100 m of shrike nests, short-grass habitats (e.g., pasture, hay fields, and residential lawns) predominated, comprising, on average, more than 80% of the area. Short vegetation around nests may result in increased prey availability. The relatively high reproductive success of Loggerhead Shrikes in this study is similar to that reported by researchers elsewhere, and it does not explain the recent decline in shrike populations in the region. *Received 29 Sept. 1988, accepted 15 Jan. 1989.*

Despite a broad distribution that extends coast to coast from southern Canada to Mexico, populations of Loggerhead Shrikes (*Lanius ludovicianus*) have recently declined over much of North America (Arbib 1972, Bystrak and Robbins 1977, Bystrak 1981, Geissler and Noon 1981, Morrison 1981, Robbins et al. 1986). Currently, the Loggerhead Shrike is listed as "endangered" in New York, Michigan, and Wisconsin; and as "threatened" or "watch" in several other states (Haas 1987). Audubon Society Christmas Bird Counts indicate that wintering populations of shrikes in southeastern Atlantic coastal states experienced a 22% decline between 1961 and 1978, the most severe decline reported for any region (Morrison 1981). Although habitat destruction has been suggested as a possible cause of population declines in both Illinois and Missouri (Graber et al. 1973, Kridelbaugh 1982), there are no studies of shrike reproductive success and habitat use in the southeastern Atlantic coastal region of the United States. Here, we (1) describe the results of a 2-year study of the nesting habitat and reproductive success in a population of Loggerhead Shrikes in north-central South Carolina, and (2) discuss our results in light of recent population declines.

STUDY AREA AND METHODS

We studied shrikes during the breeding seasons of 1986 and 1987 in the Piedmont physiographic region in central York County, South Carolina. The 33,518-ha study site consisted

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of pastures and small fields of row crops (mainly cotton, soybean, and corn) interspersed with hardwood forests and scattered residences.

From February to August each year, the study area was searched primarily from the road, and all areas where shrikes were sighted were observed intensively for signs of nesting with 7× binoculars and a 20× spotting scope. Nests were found by following the flight paths of adult shrikes carrying nest material or food. Areas where shrikes were sighted were rechecked frequently, and the first nest found in each territory was considered to represent a first nesting attempt; however, several first nests that failed early in the nesting cycle may have been missed. Nests were checked periodically to determine nesting success (% of nests that fledged at least one young), hatching success (% of eggs laid that hatched) and fledging success (% of young hatched that fledged). Nestlings that were at least 14 days old were considered to have fledged. After fledging, young were inconspicuous and difficult to find, and the number of fledglings may have been underestimated.

We observed house cats (*Felis catus*) near nests on several occasions in 1986. In 1987, each time a cat was seen in a shrike territory, we recorded its presence and distance from the nest.

In 1986, adult and juvenile shrikes were banded with a single aluminum U.S. Fish and Wildlife Service numbered leg band. In 1987, unique combinations of three plastic colored leg bands and one U.S. Fish and Wildlife Service aluminum band were placed on captured birds. The seams of colored bands were sealed with acetone to reduce the likelihood of their removal by shrikes.

Modified bal-chatri traps (Clark 1968) and bow nets baited with crickets, lab mice, or nestling shrikes were used to trap adults. The most effective method of trapping adults was to place their nestlings in bow nets within 5 m of a nest. This procedure did not appear to affect subsequent adult behavior.

To limit the disturbance of breeding birds, we waited to measure nesting habitat until after the young had fledged. After fledging, we recorded nest location (in relation to roadsides, fields, residences, hedgerows, and isolated trees), nest-tree species, and the dominant vegetation within 2.5 m of the nest tree. We defined isolated trees as trees that were separated from other trees by at least 50 m. Nest height, tree height, tree canopy width, height of the lowest branch on the nest tree, and the relative position of the nest in the tree were measured with a clinometer, meter stick, and compass. We assessed exposure of the nest tree by measuring the percent of obstruction by adjacent foliage within 1 m of the nest tree.

To assess the importance of habitat parameters in shrike territories, we estimated the percent of each habitat type within 100 m (3.1 ha) of each nest. Distance from nests to nearest fence, hedgerow, road, building, and woodlot were measured directly with a distance measuring wheel (<200 m) or were estimated (>200 m).

Measurements of the vegetation height and density within 10 m of the nest tree were taken with a Robel pole (Robel et al. 1970). Four 10-m transects, the first determined randomly, were aligned at right angles from the nest tree. Three equidistant measurements were taken along each transect for a total of 12 measurements per nest. Dominant vegetation type at each measurement site was recorded.

The direction of the nest from the tree trunk for eight first nests and seven second nests was measured with a compass.

RESULTS

We found 22 shrike nests between 17 March and 16 July 1986, and 27 nests between 24 March and 12 July 1987. We believe that these nests

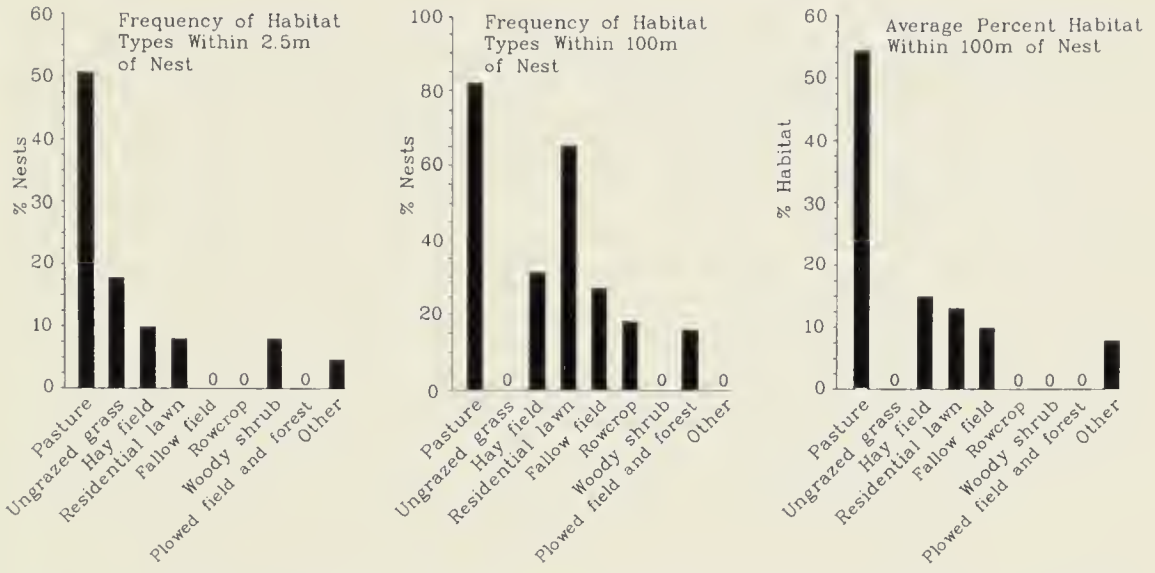

FIG. 1. Habitat types near Loggerhead Shrike nests in north-central South Carolina.

represented the majority of shrike nests in the study area each year. Thirty-seven (76%) nests were in fields of approximately 5–60 ha, and 8 (16%) were within 9 m of the center of a road. Four (8%) nests were in residential lawns. Shrikes nesting in fields and along roads usually nested in fencerows or hedgerows. All nests in residential lawns were in isolated trees. Fifty-seven percent (28) of the nests were in rows of trees or shrubs; the remaining nests were in isolated trees.

Pasture comprised an average of 54% of the habitat within 100 m of nests; hay fields, residential lawns, and fallow fields made up most of the remaining habitat. Pasture occurred within 100 m of 18 (82%) nests, and residential lawns occurred within 100 m of 16 (65%) nests. Hay fields, fallow fields, rowcrops, and plowed or forested land all were recorded less frequently. Pasture was the dominant habitat within 2.5 m of 25 nests (51%), while ungrazed grasses, hay fields, residential lawns and woody shrubs occurred less frequently (Fig. 1). Vegetation within 10 m of nests usually was low, with a mean Robel reading of 7.5 ± 6.4 cm (N = 49).

Thirty-one nests (63%) were found in red cedar (*Juniperus virginiana*), four (8%) in hackberry (*Celtis laevigata*), three (6%) in live oak (*Quercus virginiana*), two (4%) in black cherry (*Prunus serotina*), and one nest each (2%) in the following: winged elm (*Ulmus alata*), grape vine (*Vitis* sp.), holly (*Ilex opaca*), honey locust (*Gleditsia triacanthos*), white oak (*Quercus alba*), water oak (*Q. nigra*), persimmon (*Diospyros virginiana*), loblolly pine (*Pinus taeda*), and an unidentified tree.

The average nest site is depicted in Figure 2. The distance at nest height

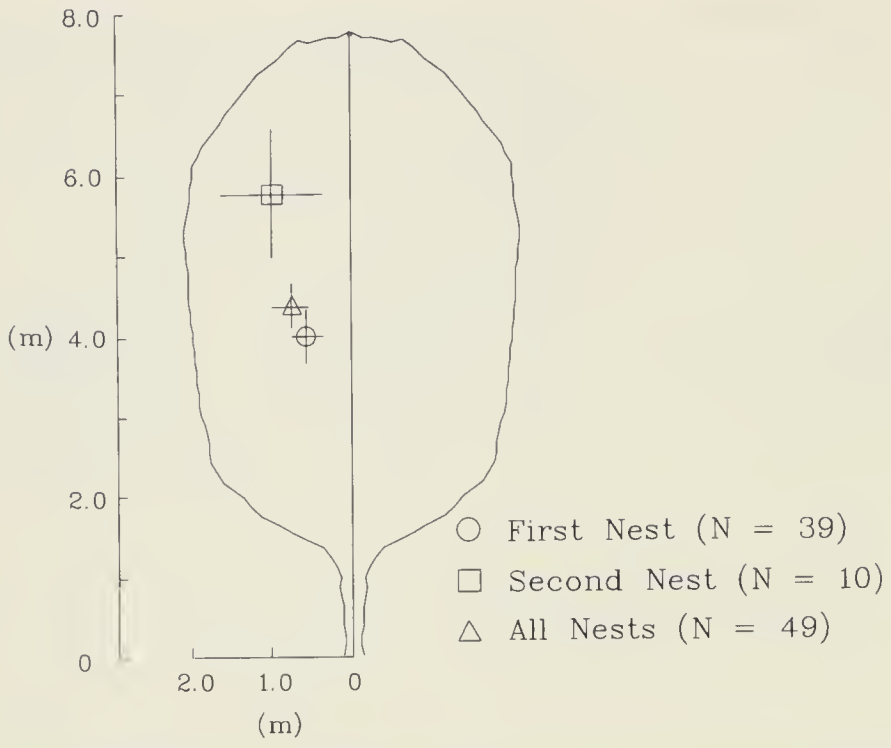

FIG. 2. Position of Loggerhead Shrike nests in trees in north-central South Carolina.

from the trunk to the canopy edge was significantly greater in 1987 than in 1986 (t-test, $t = 2.12$, df = 45, $P < 0.05$). Shrikes nested significantly higher in 1987 than in 1986 (t-test, $t = 2.09$, df = 47, $P < 0.05$), and, although nest-tree height did not differ between years (t-test, $t = 0.95$, df = 47, $P > 0.05$), relative nest height (nest height as a function of nest-tree height) also was greater in 1987 than in 1986 (t-test, $t = 2.23$, df = 47, $P < 0.05$) (Table 1).

First nests were significantly lower than were second nests ($\bar{x} = 4.00 \pm 1.99$ m, N = 39 vs $\bar{x} = 5.75 \pm 2.45$ m, N = 10, t-test, $t = 2.49$, df = 47, $P < 0.05$), and there was a nonsignificant tendency for first nests to be closer to the trunk than were second nests ($\bar{x} = 0.59 \pm 0.98$ m, N = 37 vs $\bar{x} = 1.41 \pm 1.47$ m, N = 10, t-test, $t = 1.67$, df = 46, $0.10 > P > 0.05$). The direction of the nest from the tree trunk tended to be more southerly in first nests than in second nests ($\bar{x} = 165° \pm 73$, N = 8 vs $\bar{x} = 265° \pm 72$, N = 7).

Nests were closer to utility lines (t-test, $t = 2.21$, df = 47, $P < 0.05$) in 1986 than in 1987, but there were no differences in the distances of nests to fencerows, hedgerows, roads, buildings, or woodlots between years (Table 1).

Of the 49 nests found, six (12.2%) represented second nestings following a failed first nesting, and four (8.2%) represented second nestings following a successful first nesting. Second nests were more difficult to find than

TABLE 1

NEST-SITE CHARACTERISTICS OF LOGGERHEAD SHRIKES IN NORTH-CENTRAL SOUTH CAROLINA, 1986 AND 1987

Nest-site characteristics	1986	1987	Both years	P[a]
Nest-tree exposure (%)	81.6 ± 29.8 (22)[b]	88.8 ± 16.9 (27)	85.6 ± 23.6 (49)	$P > 0.05$
Nest height[c] (m)	3.7 ± 1.2 (22)	4.9 ± 2.6 (27)	4.4 ± 2.2 (49)	$P < 0.05$
Nest-tree height	7.2 ± 2.3 (22)	8.2 ± 4.7 (27)	7.7 ± 3.8 (49)	$P > 0.05$
Relative nest height	0.5 ± 0.2 (22)	0.7 ± 0.4 (27)	0.6 ± 0.3 (49)	$P > 0.05$
Height of lowest nest-tree branch	1.4 ± 0.7 (22)	1.5 ± 1.0 (26)	1.5 ± 0.9 (48)	$P > 0.05$
Distance from trunk to:				
nest	0.5 ± 0.8 (21)	0.9 ± 1.6 (26)	0.8 ± 1.3 (47)	$P > 0.05$
canopy edge	1.4 ± 0.9 (21)	2.5 ± 2.4 (26)	2.0 ± 2.0 (47)	$P < 0.05$
Distance from nest to:				
fencerow	14.1 ± 19.3 (22)	21.7 ± 36.5 (27)	18.3 ± 30.0 (49)	$P > 0.05$
hedgerow	26.7 ± 36.8 (7)	25.9 ± 38.9 (6)	26.3 ± 36.2 (13)	$P > 0.05$
utility line	42.1 ± 40.2 (22)	75.2 ± 62.0 (27)	60.3 ± 55.4 (49)	$P < 0.05$
road	73.8 ± 68.4 (22)	95.7 ± 90.7 (27)	85.9 ± 81.4 (49)	$P > 0.05$
building	102.0 ± 68.7 (22)	133.1 ± 109.2 (27)	119.1 ± 93.6 (49)	$P > 0.05$
woodlot	226.0 ± 116.2 (22)	199.9 ± 105.2 (27)	211.6 ± 109.8 (49)	$P > 0.05$

[a] Significant difference between years using *t*-tests.
[b] $\bar{x}$ ± SD (N).
[c] All distances and heights are in meters.

TABLE 2
REPRODUCTIVE SUCCESS OF LOGGERHEAD SHRIKES IN NORTH-CENTRAL SOUTH CAROLINA, 1986 AND 1987

	1986	1987	Both years
Clutch size	5.3 ± 0.8 (6)[a]	5.2 ± 0.6 (14)	5.3 ± 0.6 (20)
Number young hatched per nest	4.8 ± 1.4 (15)	4.1 ± 1.9 (22)	4.4 ± 1.8 (37)
Number young fledged per nest	3.3 ± 2.4 (22)	2.8 ± 2.5 (27)	3.0 ± 2.5 (49)
Number young fledged per successful nest	4.6 ± 1.5 (16)	4.8 ± 1.0 (16)	4.7 ± 1.3 (32)
Hatching success	100.0% (5)[b]	92.6% (13)	94.7% (18)
Fledging success	94.4% (15)	83.5% (19)	88.3% (34)
Nesting success	72.7% (22)	59.3% (27)	65.3% (49)

[a] $\bar{x}$ ± SD (N).
[b] Mean percent (N).

were first nests, mainly because after the first brood fledged, male shrikes were often feeding up to five fledglings, as well as an incubating female, and we may have missed some of the latter feeding activity. Most renesting occurred within one week of failed nestings. First and second nests did not differ in clutch size, hatching success, nesting success, fledging success, number of young fledged per nest, or number of young fledged per successful nest; nor was there any difference among all nests from 1986 versus 1987 in these measures (all t-tests and χ^2 tests, $P > 0.05$, Table 2).

After we combined data for both years, both the number of young hatched per nest (t-test, $t = 3.22$, df = 34, $P < 0.05$) and the number of young fledged per successful nest (t-test, $t = 2.18$, df = 30, $P < 0.05$) were significantly greater for nests in red cedar than for nests in other species of trees (Table 3). And, although none of the differences were significant, shrikes nesting in red cedars had higher hatching, fledging, and nesting success than those nesting in other species of trees (Table 3).

Nesting success of shrikes nesting in isolated trees was 76.2% (N = 21), compared with 57.1% (N = 28) for nests in fence and hedgerows; however, the difference was not significant ($\chi^2 = 1.19$, df = 1, $P > 0.05$).

The nesting success of shrikes breeding within 100 m of pasture averaged 70.0%, compared with 44.4% for those that nested further from pasture ($\chi^2 = 1.18$, df = 1, $P > 0.05$), and shrikes nesting near pasture fledged 1.4 more young per nest than those nesting further from pasture (3.3 ± 2.4, N = 40 vs 1.9 ± 2.4, N = 9, $t = 1.58$, df = 47, $P > 0.05$); however, neither of these differences was significant.

In 1987 cats were observed in 10 shrike territories that had 13 nesting

TABLE 3

REPRODUCTIVE SUCCESS OF LOGGERHEAD SHRIKES NESTING IN RED CEDAR AND OTHER SPECIES OF TREES IN NORTH-CENTRAL SOUTH CAROLINA, 1986 AND 1987

	Nests in red cedar	Nests in other species of trees
Clutch size	5.4 ± 0.7 (11)[a]	5.1 ± 0.6 (9)
Number young hatched per nest	5.2 ± 0.9 (21)	3.5 ± 1.9 (15)
Number young fledged per nest	3.4 ± 2.5 (31)	2.4 ± 2.3 (18)
Number young fledged per successful nest	5.0 ± 1.1 (21)	4.0 ± 1.3 (11)
Hatching success	98.3% (10)[b]	90.2% (8)
Fledging success	90.9% (21)	83.0% (13)
Nesting success	67.7% (31)	61.1% (18)

[a] $\bar{x}$ ± SD (N).
[b] Mean percent (N).

attempts. Nesting success was 53.8% in these territories, compared with 71.4% for nests where no cats were observed ($\chi^2 = 0.29$, df = 1, $P > 0.05$).

Two shrikes were found dead on the road. One was an adult that had been dead for several days when it was found about 150 km from the study area. The other was a color-banded juvenile that had fledged the previous week from a nest 23 m from where the carcass was found. There were no utility lines or other obstructions in the area with which the fledgling could have collided. Shrike feathers were scattered along the road within 2 m of the carcass. Juveniles and adults from the nest were seen foraging along the same road.

DISCUSSION

Loggerhead Shrikes nested more frequently in red cedar, which is common in disturbed fields, than in any other species of tree. In central South Carolina, 120 km S of our study site, where red cedar is less common, shrikes also used it as a nest tree more often than any other species (Cely and Corontzes, unpubl. data). In Virginia, shrikes used red cedar and hawthorn (*Crataegus* spp.) more than expected based on availability (Luukkonen 1987). In general, red cedar appears to be a preferred nest tree for shrikes wherever shrikes and cedars co-occur (Graber et al. 1973; Siegel 1980; Kridelbaugh 1982, 1983; Luukkonen 1987). Luukkonen (1987) suggested that nests in cedar and hawthorn were more concealed than nests in other locations. In South Carolina, the amount of cover provided

by red cedar may be especially important early in the nesting season when deciduous trees have not yet leafed out. In Colorado, outside the range of red cedar, where shrikes selected thorny trees, Porter et al. (1975) hypothesized that the degree of cover a plant provided was more important than the particular species of tree. Hawthorns have thorns and red cedars have prickly needles that may discourage predators. Reduced predation due to the presence of thorns has been documented previously in a study of Long-tailed Tits (*Aegithalos caudatus*) in England (Lack and Lack 1958). In north-central South Carolina, shrikes that nested in red cedar, on average, fledged one more young per nest than did shrikes that nested in other trees (Table 3). Similarly, in Alabama, shrikes that nested in red cedar and osage orange (*Maclura pomifera*) had higher nesting success than did shrikes that nested in other tree species (Siegel 1980). Kridelbaugh (1983), however, working in Missouri, found that shrikes that nested in deciduous trees had higher nesting success than did those that nested in red cedar. In Virginia, nest success did not change with species of tree (Luukkonen 1987).

In our study first nests were significantly lower and somewhat closer to the trunks of nest trees than were second nests, a trend that has been noted by previous researchers (Kridelbaugh 1983, Luukkonen 1987, Cely and Corontzes, unpubl. data). First nests were on the southerly sides of trees more often than were second nests. Placement of nests in trees appears to be determined by the opposing factors of predation and wind (cf. Horvath 1964, Collias and Collias 1984). Shrikes are typically one of the earliest nesting passerines (Kridelbaugh 1983), and their eggs and young may be subject to periods of harsh weather (Porter et al. 1975, Kridelbaugh 1983). In Missouri, predation was the major cause of nest failure in the first breeding season studied, and high winds and rains were responsible for the greatest number of nest failures in the second breeding season (Kridelbaugh 1983). Similarly, in Colorado, although predation was the major cause of nest failure overall, hail and heavy thunderstorms accounted for 9 of the 12 failed nests in 1970 (Porter et al. 1975). In our study, early in the year, shrikes placed their nests on the south side of trees, lower and closer to the trunks. Presumably, they did so to take advantage of the less windy microclimate and greater protection from inclement weather, despite the probable increased risk of predation. Later in the year as temperatures increased, shrikes oriented their nests on the west side of trees, higher and further from the trunks, presumably to make the nest more difficult for ground predators to reach, or, possibly, to impede the development of a search image by predators (cf. Collias and Collias 1984).

Pasture was the most conspicuous habitat component, both within 2.5

m and 100 m of shrike nests (Fig. 1). Similarly, in Missouri 67% of shrike nests were surrounded by pastures (Kridelbaugh 1983). In Colorado, shrikes nested in grasslands more frequently than in cultivated areas (Porter et al. 1975); and, in Alabama, 65% of shrike nests were in hedgerows associated with pastures or cultivated fields (Siegel 1980).

Shrikes that nested within 100 m of pasture fledged 1.4 more young per nest than did shrikes that nested farther from pasture. Similarly, in Virginia shrikes were more productive in, and were more likely to reoccupy areas dominated by pastures (Luukkonen 1987). In West Germany, the number of young Red-backed Shrikes (*L. collurio*) fledged per nest was greater in pastures than in other habitats, and shrikes occupied this habitat longer than they did other habitats (Brandl et al. 1986).

Lawns and hay fields also appeared to be heavily used by shrikes in north-central South Carolina, where, when combined with pastures, these habitats occupied over 80% of the 100-m area sampled around all nests. In Missouri, Kridelbaugh (1982) reported that shrikes preferred grassy habitats (i.e., lawn, pasture, and hay fields) and avoided rowcrops when establishing breeding territories. All of these habitats provide (1) permanent grassland (i.e., land not tilled regularly), (2) routine disturbances by mowing or grazing, and (3) lower vegetation than similar undisturbed grassy habitats.

The presence of short vegetation near nests in this study was apparent from the low Robel readings obtained within 10 m of nests. In West Germany, Red-backed Shrikes that nested in pastures had increased prey available to them (Brandl et al. 1986). The American Kestrel (*Falco sparverius*), which is sometimes considered an ecological counterpart of the Loggerhead Shrike in portions of its range, exhibits reduced hunting success with increasing height of vegetation (Toland 1987).

Shrikes characteristically hunt from unobstructed perches including utility lines and exposed branches (Craig 1978). This hunting technique allows shrikes to scan the territory for predators, and, simultaneously to perform intraspecific displays and hunt for food, at a low energetic cost (Craig 1978). Increased hunting efficiency as a result of shorter vegetation would be especially important during the breeding season when adults are providing approximately 165 food items per day to their nests (Gawlik unpubl. data).

Shrikes are generalists that prey on the most abundant and obtainable food source within their dietary range (Miller 1931). Shrikes are known to capture prey flushed by farm machinery (Caldwell 1986), and in north-central South Carolina shrikes capitalize on recently plowed or mowed fields by frequently foraging in these areas soon after the disturbance. The extent to which shrikes use a recently discovered food source was made

TABLE 4
REPRODUCTIVE SUCCESS OF LOGGERHEAD SHRIKES IN NORTH AMERICA

Location	Number of nests	Mean clutch size	Nesting success (%)	Hatching success (%)	Number fledged per successful nest	Reference
Southern Illinois[a]	20	5.7	80	—	4.6	Graber et al. (1973)
Central Illinois[a]	25	5.6	71	—	4.8	Graber et al. (1973)
Colorado	77	6.4	66.2	79.5	5.4	Porter et al. (1975)
Illinois[a]	13	5.2	72.0	—	3.9	Anderson and Duzan (1978)
Alabama	37	5.0	43.2	84.7	—	Siegel (1980)
Missouri	55	5.7	69.1	85.3	—	Kridelbaugh (1982)
Virginia[a]	57	5.1	62.1	90.6	4.0	Luukkonen (1987)
South Carolina	49	5.3	65.3	94.7	4.7	This study

[a] The Mayfield method was used to calculate reproductive success.

apparent on several occasions when a clear plastic tray containing approximately 40 crickets was placed within 20 m of a nest. The adult that discovered the food source repeatedly took crickets from the tray to the nestlings until all of the crickets were gone or until the bird was captured.

Shrikes often forage and nest along roads (Robertson 1930; Miller 1931; Graber et al. 1973; Craig 1978; Luukkonen 1987; Cely and Corontzes, unpubl. data, this study), leading some researchers to suggest that collisions with vehicles are a major cause of shrike mortality (Robertson 1930, Miller 1931). Sixteen percent of shrike nests we found were in roadside hedges or fencerows less than 9 m from the center of a road, and we saw shrikes foraging in the mowed strip along roads on numerous occasions. Robertson (1930), reported that in his study area in California, shrikes were the fourth most common roadkilled species observed. Based on these observations, Miller (1931) estimated that 2–7% of that population died as a result of collisions with vehicles. In Virginia, Luukkonen (1987) reported that 17.6% of his known mortality cases were juveniles that were probably killed by vehicles. He cautioned, however, that his sample was biased towards conspicuous carcasses found on roads, and might not be representative of the population. In our study, the two known cases of shrike mortality appeared to be due to collisions with vehicles.

Predation supposedly accounts for many of the reported cases of shrike mortality (Porter et al. 1975, Kridelbaugh 1983); however, actual predation rarely has been observed. Although no incidents of predation were observed in our study, domestic cats and black rat snakes (*Elaphe obsoleta*) commonly were seen near shrike nests, and there was a non-

significant tendency for nesting success to be lower at nests where cats had been observed. Adult shrikes vigorously swooped at and hovered over cats and snakes until the intruders were out of the territory or out of sight, suggesting that both cats and snakes pose a recognized threat to shrikes.

Reproductive success of shrikes in South Carolina is similar to that reported by researchers in other areas (Table 4). Kridelbaugh (1983) suggested that, despite considerable annual variability, shrike reproductive success was still high for an open-nesting passerine in the North Temperate Zone and concluded that factors other than reproductive success were responsible for the decline of shrike populations in Missouri. Similarly, in Illinois, although shrikes had high reproductive rates, fall populations remained low (Graber et al. 1973). Productivity data from our study support the notion that shrikes are fledging high numbers of young in areas where populations are declining and they suggest that population declines in the southeastern U.S. do not result from low reproductive success.

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ANTI-PREDATORY BEHAVIOR OF LAPWINGS: FIELD EVIDENCE OF DISCRIMINATIVE ABILITIES

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ABSTRACT.—The responses of three species of lapwings (Charadriidae: *Vanellus* spp.) to various potential predators and physically similar non-predators were recorded in the field in Kenya and Venezuela to determine how responses varied with stimulus and context of encounter. Responses observed included various alarm calls, distraction displays, aggressive displays, and fleeing. Responses varied with location of predator (terrestrial or aerial) more consistently than with class of predator (mammal, bird, or reptile), although one lapwing species differentiated reptiles from other predators. Responses varied greatly with predator species and lapwing reproductive state. The results suggest that lapwings discriminate the various kinds of predators and non-predators they encounter and that responses to each correspond to the type and degree of danger each represents. Discriminative abilities appear to be more sophisticated, and false alarms much less frequent, than in domestic fowl, a difference that may be related to the more open nature of the habitats used by lapwings. Lapwings induced appropriate anti-predatory behavior from their chicks through alarm vocalizations. Except for a distinct call given to reptiles by one species, alarm vocalizations appeared to form a graded series. *Received 14 Nov. 1988, accepted 25 June 1989.*

Birds recognize their predators and respond to them in ways designed to avoid capture based on that recognition. The appropriate response varies with the species of predator and with the context of the encounter between prey and predator. Ideally a bird should avoid responding to species or individuals that do not pose a threat, and they should employ the response that will be most effective in each encounter with a dangerous individual. Such perfection, of course, is impossible to achieve. Available sensory information may be imperfect, and the stimulus situations that must be evaluated are almost infinite. Errors of different kinds have appreciably different costs: false alarms waste time and energy, but failure to respond to a predator may be fatal. How animals perceive and classify their predators and the threats that they represent is an interesting issue (Marler 1982). A related issue is the extent to which an individual may communicate its perceptions to others through responses such as alarm calls (Gyger et al. 1987).

That birds have sophisticated, complex predator recognition systems is readily evident. Countless species are known to respond to some predators with alarm calls that cause recipients to flee to cover or freeze, respond to others with calls that attract recipients and induce mobbing,

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and ignore yet others. Besides predator identity, response has been shown to vary with such aspects of the stimulus situation as stage of the reproductive cycle (Simmons 1955, Greig-Smith 1980, Patterson et al. 1980, Weatherhead 1982, Buitron 1983, Knight and Temple 1986) and predator behavior (Hamerstrom 1957, Morton and Shalter 1977, Shalter 1978). The means by which birds learn to recognize predators has been well studied by Curio (1975, Curio et al. 1978). What is lacking in the avian literature are quantitative studies of the relationships between stimulus situations and anti-predatory behavior (Gochfeld 1984) such as those on vervet monkeys (*Cercopithecus aethiops*) (Seyfarth and Cheney 1980; Seyfarth et al. 1980a, b) and ground squirrels (*Spermophilus* sp.) (Hennessy and Owings 1978; Leger and Owings 1978; Rowe and Owings 1978; Leger et al. 1979, 1980; Owings and Leger 1980; Robinson 1980, 1981; Hennessy et al. 1981). Thus information about the total perceptual strategy, its limits, and its design is lacking. How do birds classify predators, taxonomically, by location (aerial or terrestrial), according to urgency of response (Owings and Hennessy 1984, Gyger et al. 1987) or by some other means? How fine may discriminations between dangerous predators and physically similar but non-threatening species be, and do species vary in this respect? How much information about predators is communicated between individuals? Do apparent errors such as false alarms represent errors in perception, or do they merely reflect the classification system used? Answering these questions requires a holistic approach to the study of predator recognition.

The pioneering study of Gyger et al. (1987) provides a framework for such research. Gyger et al. (1987) found that domestic fowl (*Gallus domesticus*) kept in large outdoor aviaries exhibited typical terrestrial and aerial alarm calls. Classification appeared to be based more on location of stimulus than identity of stimulus. False alarms were frequent. Detailed analysis of variation in aerial alarm calls led Gyger et al. (1987) to conclude that the first element of the call served an alerting function and that the second varied with the stimulus in a way that reflected the angular size of the object projected onto the retina of the bird. The strategy of domestic fowl appears to be to detect objects of a specific angular size travelling through the air rather than making fine discriminations between stimulus species. Gyger et al. (1987) relate this strategy to the presence of a visual system adapted for a broad field of view, a favorable feature in a ground-dwelling species.

The purpose of this paper is to present data from another group of ground-dwelling birds, lapwings (*Vanellus* spp.), that, similar to data from a passerine species (Buitron 1983), suggest a perceptual strategy that differs from that of domestic fowl. The paper provides a quantitative account

of the relationship between stimulus situations and responses to add to the growing body of literature in this area (Patterson et al. 1980, Buitron 1983, Byrkjedal 1987, Gyger et al. 1987, Trail 1987, Knight and Temple 1988).

METHODS

Study sites and study populations.—I observed Long-toed Lapwings (*Vanellus crassirostris*) and Blacksmith Plovers (*V. armatus*) in Amboseli National Park, Kenya during 14 months spanning three years (July–August 1975; August 1976–July 1977; December 1978). I observed Southern Lapwings (*V. chilensis*) near Mantecal, Venezuela during April–July 1978.

Amboseli and Mantecal both are areas of flat, open savanna. The climate in both sites is characterized by highly seasonal rainfall and lack of seasonality in temperature. Annual rainfall is much greater in Mantecal (1500 mm) than in Amboseli (300 mm). The study sites are described more fully by Ramia (1967), Altmann and Altmann (1970), Western and Van Praet (1973), Troth (1979), and Walters (1982).

Like most lapwings, the species studied are conspicuous ground-dwellers of open habitats. Long-toed Lapwings in Amboseli lived primarily on surface vegetation on marshes, whereas Blacksmith Plovers inhabited areas of short grass or sedge at the edges of marshes and waterholes. Southern Lapwings occupied habitat in Venezuela similar to that occupied by Blacksmith Plovers in Kenya. Most observations in Amboseli were made along Enkongo Narok Swamp, a permanent spring-fed body of water. Observations in Mantecal were made in privately owned cattle fields and in a government-owned livestock area containing many impoundments.

Sampling methods.—Based on ease of access and observability, I selected 10–20 pairs from each of the three lapwing populations for intensive observations. Sampling was rotated among these pairs so that all were sampled approximately equally often at all times of day. Pairs were identified by location (these are territorial species), and in the cases of Southern and Long-toed lapwings, by variations in plumage features.

Responses to predators were sampled by focal sampling (Altmann 1974), using a vehicle as a blind. Samples included one or two pairs of lapwings as subjects. Samples taken in Kenya were 15 min in duration, whereas those taken in Venezuela were 10 min in duration. Because these species are tame, conspicuous, and in open habitats, subjects were rarely out of sight during samples (4% of time in Venezuela, <1% in Kenya). Birds held territories long before and after breeding, so that responses of non-breeding territorial birds, as well as breeding birds, could be sampled.

I collected nearly 300 pair-hours of focal samples. I also collected ad lib samples (Altmann 1974) from flocks of non-territorial birds during both the breeding and non-breeding seasons and from pairs other than those intensively sampled throughout the breeding cycle. Because responses to predators were not apparently different during focal and ad lib samples, I combined the two kinds of data in the analyses, producing a sample of over 700 encounters with potential predators.

I considered all large reptiles, mammals, and birds to be potential predators for sampling purposes. Each time a potential predator entered the study area, I recorded the responses of the focal birds. I use Gochfeld's (1984) terminology to classify responses observed. When possible, I noted the distance between predator and responding bird when the response began, as well as the distance between the predator and any nest or young. I noted distances for each successive response elicited by a particular predator. Maps of the study areas facilitated estimating distance.

Recordings of alarm calls were made using Scotch tape 208, a Nagra III tape recorder,

and a Sennheiser MKH 804 directional microphone. Sound spectrograms were prepared on a Kay Sona-Graph 7029A using a wide-band filter.

RESULTS

Southern Lapwings

Response repertoire.—Lapwings appear to be exceptionally vigilant birds. Responses to those potential predators that evoked responses routinely began while the stimulus animal was well over 100 m from the birds. The initial response to a potential predator was often vigilant posturing and calling, but many encounters escalated to include more dramatic responses. Incubating birds regularly exhibited early surreptitious departure, quietly running from the nest in a crouched position. Other responses observed included two forms of attack, mobbing, crouched run, false brooding, injury-feigning, and ungulate display.

One of the forms of attack (pecking attack) also was limited to interactions with reptiles. In this display, the wings were held high as the bird struck at the potential predator with its bill and feet. The second form of attack consisted of swooping low over the stimulus animal. An odd click-like sound occurred as the bird passed over its victim, but I never observed the bird actually strike the victim. False brooding and crouched run were common responses, and the latter appeared to function as a distraction display. The performer was quite vocal and ran toward or parallel to the stimulus animal as well as away from it. Injury-feigning was rare and consisted of taking hobbling steps, either while dragging one trailing wing held out at an awkward angle, or while in a crouched posture with both wings spread. In the ungulate display, the bird spread its wings up over its back, exposing the boldly colored underwings, while standing in a slight crouch with its head held low. Often the bird lunged at the stimulus animal.

Vocalizations.—Behavioral responses typically were accompanied by vocalizations. Vigilant posturing was accompanied by a call employed in several other contexts such as when conspecifics approached the territory. This alerting call usually elicited no obvious response from chicks, if present, but sometimes induced very young chicks to crouch. Two additional alarm calls were given. The first (Fig. 1A) was commonly heard. It was given by birds standing in a vigilant posture and also accompanied crouched run, injury-feigning, false brooding, and swooping attack. This call appeared to grade into the alerting call. The individual notes sounded harsher, more intense and longer, with the ending less distinct than the notes of the alerting call. The notes of the alarm call may have been characterized by greater frequency modulation as well. By further changes in these same parameters, this alarm call graded into a call that attracted

FIG. 1. Alarm call (A) and mobbing call (B) of the Southern Lapwing.

conspecifics to produce a mobbing response (Fig. 1B). It attracted not only territorial neighbors but also non-territorial vagrants, and all joined the calling birds in attacks, false brooding, crouched runs, and injury-feigning. When the danger passed, the residents vigorously evicted the attracted birds from their territory.

The first alarm call was bewilderingly variable. In addition to the variation involved in gradations with alerting and mobbing calls, there was variation in the pitch of the call and its tempo. I did not obtain sufficient recordings to analyze this variation, structurally or functionally. That

chicks, out of sight of the potential predator, responded to some calls by crouching instantly and to others, invariably ones given to mammals, by first running to cover and then crouching, indicates that at least some of this variation may be functional.

The second alarm call (reptile alarm call) was heard infrequently and was not recorded. This call occurred only during interactions with reptiles, accompanying pecking attack, and caused chicks to move rapidly away from the source of the call and remain upright and alert. It sounded more like the call used by parents when leading young than like the other alarm calls.

Variation in response.—Southern Lapwings exhibited three distinct types of responses to potential predators which were marked by the following behaviors: (1) reptile alarm call and pecking attack, (2) alarm call, swooping attack, injury-feigning, and mobbing, and (3) ungulate display. Alerting calls and vigilant posturing sometimes preceded all three types of response, and crouched run and false brooding regularly accompanied all three. The potential predators eliciting the first and third types of responses corresponded to taxonomic groups. The first type of response was directed only toward reptiles, and it was the only type of response given toward reptiles (11 cases). The third type of response was given only toward cows (7 cases), and it was the only type of response given to cows.

I observed only birds tending chicks responding to reptiles. There was some indication that all reptile species were not responded to equally. By far the most intense response witnessed was during the only observed encounter with the large predatory lizard *Tupinambis*. The response included repeated pecking attack, much false brooding, and prolonged reptile alarm. In contrast, responses to spectacled caimans (*Caiman crocodilus*) and iguanas (*Iguana iguana*) consisted of sporadic reptile alarm and occasional false brooding.

I observed only incubating birds performing the type 3 response, and only in the immediate vicinity of the nest. The birds inhabited fields used for grazing cattle, and thus constantly encountered cattle but ignored them except when they were in the immediate vicinity of an active nest. Horses, although less numerous than cattle, were also frequently encountered by the birds, and they, too, were ignored. I did not observe horses in the immediate vicinity of an active nest, however. Once a group of horses ran toward a pair of birds tending downy young, eliciting a type 2 response. Twice, I observed pigs in the vicinity of birds tending young, and both times an intense type 2 response was given, although the pigs never approached closely. The contrast in responses indicates that pigs were not classified with cows and horses by lapwings.

A variety of avian and mammalian species elicited type 2 responses.

Although the behavior of chicks indicates that adult responses to terrestrial and aerial predators may differ, most likely in some aspect of alarm calling, I was unable to document this. Three variables affecting response were evident: (1) stage of the reproductive cycle, (2) location of the potential predator, and (3) species of potential predator. To analyze the results, I subdivided the data according to these three variables to the extent that sample size would permit. The reproductive stages used are: (1) incubation, (2) tending small young (unable to fly, age 1 day to 6–8 wk), (3) tending large young (able to fly, age 6–8 wk to 5 mo), (4) territorial (defending territory but without eggs or young). The predator location categories used are (1) on the ground or perched near the ground, (2) flying near (<25 m) the ground, and (3) flying or soaring high (>25 m) above the ground. The two commonly observed mammalian species, dogs and humans, could be analyzed individually, but avian predators had to be grouped into the following classes due to small sample sizes: (1) caracaras (*Polyborus plancus* and *Milvago chimachima*), (2) hawks and falcons (*Buteo albicaudatus, B. magnirostris, Buteogallus urubitinga, Busarellus nigricollis, Falco femoralis*), and (3) kites and vultures (*Elanus leucurus, Rostrhamus sociabilis, Coragyps atratus, Cathartes aura, C. burrovianus*). I divided encounters into those in which a clear alarm response occurred (alarm call, crouched run, false brooding, mobbing, swooping attack) and those in which no response or only responses that were not clearly an alarm (vigilant posture, alerting call) occurred. I compared responsiveness among stages, among predator location categories, and among species by Chi-square tests comparing the frequencies of clear alarm response and no alarm response.

Sample size for birds tending large young was insufficient (9 encounters) for detailed analysis. The few responses observed were similar to those given by adults tending small young in equivalent contexts. Sample size for the territorial stage was also small (30 encounters). Responsiveness generally was low in this stage, but clear alarm responses were given to humans (6 of 12 encounters), caracaras (3 of 4 encounters with *Polyborus*, 0 of 3 encounters with *Milvago*) and one species of hawk (*Buteogallus*, 1 of 1 encounters). Several species that regularly elicited a clear alarm response during other stages did not during the territorial stage (dogs, 2 encounters; other hawks and falcons, 4 encounters).

There were several species to which lapwings were more responsive when tending small young than when incubating (Table 1). These included dogs ($P < 0.05$) and hawks and falcons ($P < 0.001$, combining all predator location classes). Lapwings were equally responsive to caracaras and to humans, both on foot and on horseback, during these two stages, and were equally unresponsive to vulture and kites. The lapwings were more

TABLE 1
RESPONSES OF SOUTHERN LAPWINGS TO POTENTIAL PREDATORS

Stage of reproductive cycle	Predator location	Predator type	Frequency of response: No clear alarm response	Frequency of response: Clear alarm response
Incubation	Flying high	Caracaras	3	1
		Kites, vultures	10	0
		Hawks, falcons	6	0
	Flying low	Caracaras	3	4
		Kites, vultures	6	0
		Hawks, falcons	6	0
	Ground, perched	Caracaras	0	2
		Kites, vultures	5	0
		Hawks, falcons	6	0
		Dogs	7	3
		Humans on foot	15	24
		Humans on horseback	8	3
Tending small young	Flying high	Caracaras	3	4
		Kites, vultures	10	0
		Hawks, falcons	2	10
	Flying low	Caracaras	2	4
		Kites, vultures	12	5
		Hawks, falcons	0	4
	Ground, perched	Caracaras	0	10
		Kites, vultures	2	0
		Hawks, falcons	1	1
		Dogs	3	17
		Humans on foot	27	90
		Humans on horseback	6	10

responsive to caracaras on the ground or perched than caracaras in flight when tending small young ($P < 0.05$), and there was a trend in this same direction during incubation (Table 1). They were less responsive to vultures and kites flying high than vultures and kites flying low, perched or on the ground when tending small young ($P < 0.05$). They were equally unresponsive to hawks and falcons and vultures and kites regardless of predator location during incubation, and were equally responsive to hawks and falcons in all predator locations when tending small young.

The birds were not equally responsive to all avian species either during incubation or when tending small young ($P < 0.001$ in both cases, combining all predator location categories). They were more responsive to

caracaras than to all other species during incubation, and less responsive to vultures and kites than all other species when tending small young. These results were significant within predator location category for both the flying low ($P < 0.05$) and flying high ($P < 0.001$) categories. Although the lapwings tended to be more responsive to humans than to dogs during incubation (Table 1), this trend was not significant ($0.05 < P < 0.1$). The birds were more responsive to humans on foot than to humans on horseback during incubation ($P < 0.05$), but not when tending small young.

Long-toed Lapwings

Response repertoire.—Adult Long-toed Lapwings responded to potential predators in similar ways to Southern Lapwings, although their response repertoire was smaller. Like Southern Lapwings, Long-toed Lapwings exhibited vigilant posturing and an alerting call (Fig. 2A) that was given in many contexts in addition to encounters with predators. This call did not elicit crouching from chicks. More intense responses observed were alarm calling and swooping attack. Alarm calls elicited crouching from chicks. They appeared to grade into the alerting call, the notes being longer, louder, and more frequent than those characterizing the alerting call (Fig. 2B). Long-toed Lapwings also exhibited an escape response in which they flew out over the open water, hovering just above the surface or occasionally performing swift, twisting evasive flight.

Variation in response.—I again divide encounters into those that resulted in a clear alarm response (alarm calling, swooping attack) versus those that did not (no response, vigilant posturing and alerting call only). I separated escape responses from these as a third category. Long-toed Lapwings gave clear alarm responses only to avian predators. I observed four encounters with jackals (*Canis aureus* and *C. mesomelus*) and four encounters with Rock Pythons (*Python sebae*), and repeatedly approached the edges of Long-toed Lapwing territories myself, but witnessed no swooping attacks or alarm calling, or escape responses. Adults and chicks approached pythons swimming or resting in their territory, but their reaction in no way suggested mobbing. One chick sat, apparently sleeping, within 0.5 m of a python for nearly an hour.

Small sample sizes precluded detailed analysis of variation in response to avian predators (Table 2). Effect of predator location could not be examined, and for only one group, harriers (*Circus* spp.) could I test for variation among stages of the reproductive cycle. Long-toed Lapwings were highly responsive to harriers, giving either an alarm or escape response in nearly all encounters with them, but there was no difference in response between birds tending eggs or young and those without eggs or young (Table 2). Species of potential predator had a noticeable effect on

FIG. 2. Alerting call (A) and alarm call (B) of the Long-toed Lapwing.

response. The lapwings never gave a clear alarm or escape response to vultures (primarily *Gyps bengalensis* or five other species), although they were present soaring overhead so often that sampling encounters with them were unnecessary. The only clear alarm responses given to groups of circling vultures were to those few groups that included a Tawny Eagle (*Aquila rapax*) (Table 2). Long-toed Lapwings more often responded to harriers than to Fish Eagles (*Haliaeetus vocifer*) or harrier-eagles (primarily

TABLE 2
RESPONSES OF LONG-TOED LAPWINGS TO POTENTIAL PREDATORS

Stage of reproductive cycle	Predator type	Frequency of response		
		No response	Alarm calling	Escape response
Tending eggs or young	Fish Eagle	3	2	0
	Harrier	1	17	6
	Falcon	0	2	3
	Tawny Eagle	0	1	0
	Harrier-Eagle	4	0	0
Not tending eggs or young	Fish Eagle	5	1	0
	Harrier	2	9	9
	Falcon	0	0	2
	Tawny Eagle	1	1	0
	Harrier-Eagle	7	0	0

Terathopis ecaudatus, or *Circaetus* spp.) both when tending eggs or young and when eggs and young were absent ($P < 0.05$ in all cases, combining clear alarm and escape responses). Although sample sizes were insufficient for analysis, the data hinted that falcons (large *Falco* spp.) and Tawny Eagles elicited responses more frequently than Fish Eagles or harrier-eagles (Table 2). I also observed encounters with kestrels (*Falco tinnunculus*) (N = 2), which were ignored, and White-browed Coucals (*Centropus superciliosus*) (N = 3) which elicited clear alarm responses.

Blacksmith Plovers

Response repertoire.—The responses exhibited by Blacksmith Plovers were similar to those observed in the other two species. Blacksmith Plovers employed vigilant posturing, an alerting call, an alarm call, swooping attack, crouched running, false brooding, ungulate display, and escape response. The form of all of these behaviors was similar to that described above for Southern Lapwings and Long-toed Lapwings. As in the other species, the alerting call and alarm call appeared to grade into one another (Fig. 3A and B). The latter, but not the former, induced the young to crouch, and the former was given in many contexts other than encounters with potential predators. In this species, a primary difference between the two calls appeared to be that the notes were shorter in the alarm call. There may have been functional variation among alarm calls as well. Notes of calls given to aerial predators (Fig. 3D) appeared to be even shorter than those of calls given to terrestrial predators (Fig. 3C). The number of calls recorded was not sufficient to investigate this variation.

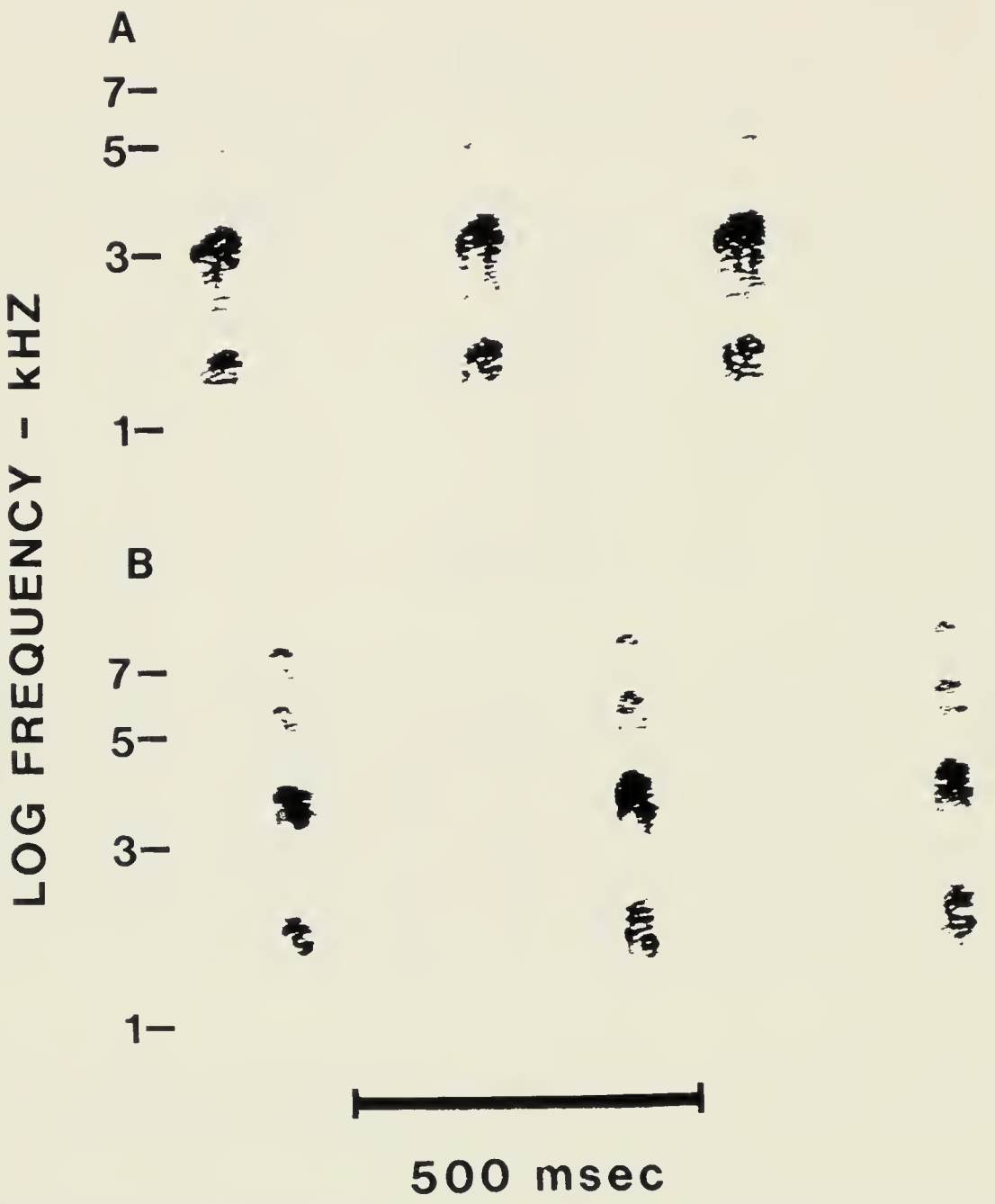

FIG. 3. Alerting call (A) and alarm call (B) of the Blacksmith Plover. (C) Alarm call given to a terrestrial predator. (D) Alarm call given to an aerial predator.

Variation in response.—Blacksmith Plovers exhibited three distinct types of response to potential predators: (1) ungulate display, (2) alarm responses characterized by alarm calling, swooping attack, and escape response, and (3) alarm responses characterized by alarm calling, crouched running, and false brooding. The third type of response was seen only in the three encounters with Rock Pythons observed. Other than these instances, I recorded crouched running and false brooding only in a few of the many

encounters with baboons (*Papio cynocephalus*) observed. Responses to baboons otherwise were type 2. None of the birds responding to rock pythons was tending eggs or young.

Only incubating birds performed ungulate display. I observed it directed toward wildebeest (*Connochaetes taurinus*) and toward me and received unconfirmed reports of responses to elephants (*Loxodonta africana*). Wildebeest were ignored by non-incubating birds. Non-incubating birds often ignored me, but those tending young gave alerting calls and led their young away from me.

Variation in alarm responses was more difficult to analyze than in other

TABLE 3
RESPONSES OF BLACKSMITH PLOVERS TO POTENTIAL PREDATORS

Stage of reproductive cycle	Predator type	Frequency of response			
		No response	Alert calling or alarm calling	Swooping attack	Escape response
Tending eggs or young	Harrier-Eagle	3	8	0	0
	Fish Eagle	0	2	1	0
	Tawny Eagle	0	9	0	0
	Harrier	0	4	3	2
	Falcon	0	0	0	1
Not tending eggs or young	Harrier-Eagle	0	1	0	0
	Fish Eagle	9	0	2	0
	Tawny Eagle	1	1	0	0
	Harrier	6	2	5	1
	Falcon	0	0	0	1

species because it was harder to distinguish clearly alerting and alarm calls. Therefore, I do not separate responses that included only alerting calls from those that included alarm calling and distinguish responses that included swooping attack from those that included only alarm calling. Responses to terrestrial predators almost always included swooping attack in addition to calling. Encounters with terrestrial predators observed included one with a Secretary Bird (*Sagittarius serpentarius*), two with jackals, and innumerable encounters with baboons recorded during 1470 h spent following baboon groups while working on another research project. The attacks on jackals and many of those on baboons were performed by birds that were not tending eggs or young.

Like Long-toed Lapwings, Blacksmith Plovers generally ignored vultures which were overhead almost constantly. With only two exceptions, calling was elicited by only those groups of soaring birds that included a Tawny Eagle. Results of encounters with those aerial predators to which Blacksmith Plovers responded are presented in Table 3. Blacksmith Plovers were more responsive to both eagles ($P < 0.001$, combining all three types of eagle) and harriers ($P < 0.05$) when tending eggs or young than when without eggs or young. However, birds without eggs or young sometimes performed swooping attacks. Among birds tending young or eggs, responses to harriers differed from responses to eagles ($P < 0.05$), more often including swooping attack or escape response. This may have been due, at least in part, to a difference in predator location, as all harriers encountered were flying low, whereas 17 of 23 eagles encountered were

flying high. Responses to the two types of predators by birds without eggs or young were not significantly different. Falcons elicited escape response in both observed encounters, a response otherwise given only rarely in response to harriers (Table 3).

DISCUSSION

Predator Recognition Strategy

The perceptual strategy used by lapwings in predator recognition appears to differ substantially from that reported for domestic fowl by Gyger et al. (1987). Lapwings gave false alarms much more rarely and appeared to make finer discriminations among stimulus species. Although more data are needed to substantiate many apparent trends, it appears that variation in lapwing responses matches rather precisely variation in the danger represented by different stimulus contexts (see below). In this respect, it appears similar to the strategy of vervet monkeys (Seyfarth and Cheney 1980; Seyfarth et al. 1980a, b) and ground squirrels (Hennessy and Owings 1978; Leger et al. 1979, 1980; Owings and Leger 1980; Robinson 1980, 1981; Hennessy et al. 1981; Owings and Hennessy 1984). The lapwing strategy seems to be to assess accurately each stimulus situation and then respond accordingly. Response time under this strategy presumably is slower than that under the strategy of the domestic fowl, which emphasizes rapid detection over a broad field of view. I suggest that this difference in strategy is related to differences between the two kinds of birds in the nature of interactions with predators. The wild ancestors of domestic fowl inhabited places in which obscuring vegetation limited their visual range. Furthermore, ground-dwelling phasianids rely on reaching cover rather than maneuverability in the air to escape predators. The cost of a false alarm in this species is presumably small because encounters with predators are brief. On the other hand, the consequences of failing to respond quickly to a predator may be fatal, because little time exists in which to correct the mistake, and delays in responding greatly reduce ability to escape. A response strategy that emphasizes quick response at the expense of fine discrimination might characterize most species living in closed environments, such as forests, for similar reasons. Trail (1987) reports a high frequency of false alarms in Cock-of-the-Rock (*Rupicola rupicola*), a species that inhabits dense forest.

The lapwings studied, on the other hand, typically have a long visual range unimpeded by vegetation in the environments in which they are found. Large birds in flight are almost constantly in view, and most can be seen long before they come within attacking distance. False alarms in such environments would be frequent and prolonged, and therefore costly,

whereas the consequences of failing to respond to a predator immediately are trivial because ample time exists to correct the mistake. In addition, lapwings are sufficiently strong fliers that they likely can escape most predators in flight, and thus allow them a closer approach than can domestic fowl. A perceptual strategy that minimizes false alarms appears well suited for species with such a life history. Buitron (1983) provides data from another species of open country, the Black-billed Magpie (*Pica pica*), that suggest an anti-predatory strategy similar to that of lapwings. She also documents fine discriminations within classes of predators and apparently adaptive changes in responses to particular species over the breeding cycle.

Lapwings appear to classify potential predators by a combination of taxonomic and urgency of response criteria. Southern Lapwings distinguished reptiles from non-reptiles, and Long-toed Lapwings were unresponsive to mammals. On the other hand, Southern Lapwings responded similarly to mammal and bird species, as did Blacksmith Plovers. In these latter cases, although the general response to different taxa was similar, additional taxonomic distinctions could have been expressed in variation in alarm calls that I could not perceive. Many discriminations made by lapwings are difficult to reconcile with any means of classification based on generalization of taxonomic cues, however. For example, Southern Lapwings responded to pigs and cows very differently, yet responded to my vehicle in the same manner as to cows. These observations are more consistent with a scheme in which species are identified individually and classified according to an urgency of response scheme. For example, a scheme consistent with my observations is that any species will elicit an ungulate response if it approaches a nest closely; others (e.g., vultures) will elicit an alarm response only if in the immediate vicinity of the young, while others will elicit an alarm response at long distances.

Adaptive Nature of Variation in Response

Variation in type of response.—Evidence of an adaptive match between response and stimulus context exists in several aspects of variation in response to potential predators. The species that elicited only ungulate display were herbivorous species that might step on and crush eggs or small young but otherwise were no threat to lapwings. Pigs, on the other hand, elicited an alarm response. This may represent a false response, but pigs are omnivores and it is conceivable that they might consume lapwing eggs or even small chicks. That a shorebird could be as unresponsive to mammalian predators as Long-toed Lapwings appeared to be is extraordinary, yet this too may be adaptive, since mammals may pose no threat to a species that inhabits surface vegetation over water. Southern Lapwing

chicks responded to reptile alarm by remaining mobile and alert, a more appropriate response than the crouching elicited by the usual alarm call because reptiles could more easily locate and capture a stationary chick than a moving one.

If the response system of lapwings is as fine-tuned as I suggest, one expects to find a difference in response to terrestrial and aerial predators. Although lapwings do not have distinct alarm calls for terrestrial and aerial predators as many birds do, it is possible that some of the apparent variation in alarm call structure differentiates terrestrial and aerial predators.

Variation among species of potential predator.—Without accurate information about the diets of the species of potential predators, it is difficult to determine whether variation in lapwing response accurately reflects variation in the threat posed by the various predator species. Only baboons were actually observed preying on lapwing eggs, and no species was observed to take chicks or adults. The diets of the potential predators are known only in general terms (Steyn 1965, 1973; Brown and Amadon 1968; Voous 1970; Brown 1971; Smeenk 1974; Picozzi 1978). Considering the general foraging habits of the species involved, nothing I observed is inconsistent with the hypothesis that lapwings are able to identify each species of potential predator that they encounter and respond to it precisely according to the danger it represents to them. Vultures and kites are unlikely to prey on eggs, young, or adults, and lapwings generally ignored them, responding to them only when they flew very close to chicks. Species to which the lapwings responded strongly, such as caracaras, falcons, and harriers are likely predators of lapwings. Southern Lapwings ignored the fish-eating specialist *Busarellus nigricollis* but responded strongly to other large hawks.

That lapwing responses accurately reflect the danger a particular potential predator poses requires several suppositions that are not obvious from what is known of the general foraging habits of the predators. Humans in Africa must be much less inclined to harm lapwings and their eggs and young than humans in Venezuela. Harrier-eagles and Fish Eagles must not be a threat to Long-toed Lapwings, whereas Tawny Eagles must be. Variation in response might also reflect variation in the effectiveness or risk of the response across predator species (Simmons 1955, Elliot 1985, Knight and Temple 1988). In this study, these aspects likely affect the form of the response, and unmeasured details such as approach distance, but not the consistency of response. That is, those species that were ignored do not appear to be sufficiently different from those to which the lapwings responded that increased risk or decreased effectiveness could have inhibited responding.

Some of the variation in response among predator species requires considerable discriminatory abilities. For example, the African species ignored vultures, yet responded to Tawny Eagles, which are similar to vultures physically and in flight pattern and often fly with them. That lapwings may possess unusual abilities in this regard has been suggested by others (Meinertzhagen 1954, Bannerman 1961). But evidence is mounting that many species may make such subtle discriminations in their anti-predatory behavior (Zimmerman 1976, Ficken and Witkin 1977, Grubb 1977, Buitron 1983, Bump 1986), although some species appear to be poor discriminators (Mueller 1976).

How such subtle discriminations might be learned is an interesting issue. Associative learning is one possible mechanism. In this regard, the behavior of lapwings in zoological parks may be revealing. At the Lincoln Park Zoo in Chicago, Spurwing Plovers (*V. spinosus*) have learned to distinguish zookeepers who take their eggs from other humans (K. Bell pers. comm.). They attack the uniformed keepers the moment they enter their large aviary, whereas they ignore zoo visitors passing within a few meters of their nest. But associative learning is too dangerous a mechanism for developing some of the discriminations exhibited by lapwings. Cultural transmission of predator recognition, which has been demonstrated in other birds (Curio et al. 1978), is a likely, less risky alternative.

Variation over the reproductive cycle.—Considerations related to parental investment may account for some variation in responsiveness to predators over the reproductive cycle (Knight and Temple 1986). But neither this nor any other general change in motivation (Simmons 1955) can account for changes in responsiveness that are not uniform across predator species. That changes in responsiveness to predators across reproductive stages match dangers posed by predators has been reported previously (Patterson et al. 1980, Buitron 1983). In this study, Southern Lapwings became more responsive to species likely to take young but not eggs (hawks, falcons, possibly dogs) when their eggs hatched, but began responding to those species that are likely to take eggs (humans, caracaras) during incubation. Caracaras are notorious scavengers, and humans in the region of the study consume lapwing eggs. It is also interesting that non-breeding Southern Lapwings remained responsive only to caracaras, which are known to prey on adults (Myers 1978), and humans who frequently threw rocks at adults.

Long-toed Lapwings and Blacksmith Plovers remained more responsive to a greater variety of species when not breeding than did Southern Lapwings. Perhaps most of these species prey on adult lapwings, but this is unlikely for at least some species, for example, baboons. Baboons regularly elicited intense versions of responses such as false brooding, normally associated with breeding, from birds that were not even holding a territory.

Perhaps these responses are non-functional mistakes. Another hypothesis is that such behavior disguises the presence of young from an intelligent predator. I also observed Crowned Lapwings (*Vanellus coronatus*), another lapwing species in Amboseli subject to baboon predation, to direct elaborate anti-predatory behavior at baboons when not breeding.

Communication Between Adults and Chicks

Part of the anti-predatory behavior of lapwings is to communicate, through vocalizations, information that enables chicks to take appropriate action. All species studied employed alarm calls that induced young to crouch, and Southern Lapwings gave an additional reptile alarm call that triggered evasive action by chicks. The dichotomous signal-response system of Southern Lapwings may represent semantic communication (Altmann 1967; Seyfarth et al. 1980a, b). Otherwise, there was no obvious communication of predator identity.

Lack of discrete calls does not necessarily mean that communication of alarm is simple, however. The graded vocalizations of lapwings in theory permit elaborate communication between adults and young. Gradations in alarm calls given by ground squirrels provide information about predator identity and subtleties of context that reflect degree of danger, and there is evidence that recipients use this information to vary their response to alarm in an adaptive manner (Leger and Owings 1978; Rowe and Owings 1978; Leger et al. 1979, 1980; Owings and Leger 1980; Robinson 1980, 1981; Hennessy et al. 1981). The communication between adult lapwings and their chicks may be equally complex. A similar potential has been suggested for graded alarm vocalizations in Carolina Wrens (*Thryothorus ludovicianus*) (Morton and Shalter 1977) and exists for many other species (Buitron 1983, Brown 1985, Knight and Temple 1988), but such communication has yet to be demonstrated in birds. There were hints of it in the responses of Southern Lapwing chicks to alarm calls. Young consistently ran to cover before crouching when adults gave alarm calls to terrestrial predators, but they crouched immediately when adults gave alarm calls to aerial predators, even when the chicks themselves could not possibly see the predator. A detailed spectrographic analysis of lapwing alarm vocalizations will be necessary to determine if this response difference corresponds to vocal gradations. Graded systems such as these are common in birds (Adret 1982), and determining their functional significance is a major outstanding research problem (Miller 1979).

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ONTOGENY OF THERMOREGULATION IN RED-TAILED HAWKS AND SWAINSON'S HAWKS

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ABSTRACT.—Nestling Red-tailed Hawks (*Buteo jamaicensis*) and Swainson's Hawks, (*B. swainsoni*), exposed daily to ambient temperatures of 5 and 16°C, showed gradual thermoregulatory improvements that most closely correlated with nestling age, the log of nestling age, or the log of nestling mass. Although thermal stability improved with increasing body size, the near normal thermoregulatory development of runt nestlings indicates that endothermy is primarily attained through factors other than body size. When nestlings were exposed to a radiation load of 1 cal/cm^2/min and rising ambient temperatures, their abilities to control rising body temperature were not highly correlated with age or four other growth parameters. In the wild, hyperthermia is probably a greater threat to these cold-hardy nestlings than is hypothermia. *Received 20 Jan. 1989, accepted 15 April 1989.*

The pattern of transition from ectothermy to endothermy among nestling birds shows much interspecific variability (O'Connor 1984). Thermal extremes encountered by nestlings of many species may be a major obstacle to nestling survival.

The ontogeny of thermoregulation in nestling diurnal birds of prey is poorly known in spite of the relative abundance of information on raptor breeding biology (Newton 1979). In this study our objective was to determine the patterns of endothermic development in young Red-tailed Hawks (*Buteo jamaicensis*) and Swainson's Hawks (*B. swainsoni*). In northern Utah, the nestling periods of Red-tailed Hawks (RT) normally span approximately 10 weeks from the earliest hatchings in late April to the latest fledglings in early July. Nestlings are sometimes exposed to relatively cool conditions (e.g., air temperatures near freezing, high winds, and rainstorms) during this period when they are dependent on the adults for food and thermal protection. The nestling period of the Swainson's Hawk (SW) is about one month later in northern Utah with earliest hatchings in early June and latest fledgings in mid August. During these nestling periods young hawks in unshaded nests can face the thermoregulatory challenge of heat stress caused by intense, direct solar radiation and air temperatures above 30°C.

METHODS

The hawk nestlings investigated during this study (6 RT and 10 SW) were obtained from nests in 1979 in northern Utah (Cache Valley, elev. 1340 to 1524 m).

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TABLE 1

ENVIRONMENTAL CONDITIONS DURING TESTS OF NESTLING THERMOREGULATORY ABILITY. AMBIENT TEMPERATURE INCREASED DURING TEST 3 FROM THE INITIAL TEMPERATURE (I) TO THE FINAL TEMPERATURE (F)

		Test conditions		
		Ambient temperature (°C)	Duration (min)	Artificial radiation (cal/cm²/min)
Test 1				
Red-tailed Hawk		16.2	30	trace
Swainson's Hawk		15.7	30	trace
Test 2				
Red-tailed Hawk		5.4	30	trace
Swainson's Hawk		5.5	30	trace
Test 3				
Red-tailed Hawk	I	12.7	20	1
	F	22.7		
Swainson's Hawk	I	12.1	20	1
	F	23.9		

Testing of thermoregulatory performance.—Nestlings were randomly selected in pairs from nests containing three young estimated to be less than one week old (except in the case of two RT nestlings estimated to be 12 and 8 days old). Ages of the nestlings were estimated from their body weights during the first 24 h of captivity by comparing with weights of wild, known-age young. Nestlings were kept on an artificial nest (70 cm × 100 cm) of sticks and shredded bark within a walk-in environmental chamber. A carpeted stove pipe, heated to a stable surface temperature of 38°C by light bulbs mounted inside, was accessible to the nestlings for heat.

Air temperature within the environmental chamber was maintained at 16 ± 2°C, except during the thermoregulatory tests described below. Humidity within the chamber was not controlled or monitored and photoperiod was similar to that occurring naturally in northern Utah during May and June (i.e., 15 h light : 9 h dark), except that it was shifted 2 h later than normal. The nestling food was a mixture of domestic hamsters and black-tailed jackrabbits (*Lepus californicus*); the head, stomach, and intestines were removed before grinding in a Waring blender.

Prior to the first feeding each morning, we measured four growth parameters on each nestling. Body weight was measured to the nearest 0.1 g with an Ohaus triple beam balance. Length of the tarsus and of the seventh primary feather was measured to the nearest 0.1 mm with a dial caliper in the standard manner (Baldwin et al. 1931). Thickness of the downy plumage along the dorsal midline between the bases of the wings was measured with a dial caliper to the nearest 0.1 mm.

Thermoregulatory performance of the nestlings was tested daily by exposing them to three sets of conditions (Table 1) which simulated thermal environments encountered by raptors nesting in northern Utah. Tests 1 and 2 were designed to determine nestling endothermic capabilities at moderately cool (16 ± 2°C) and cold (5 ± 1°C) air temperatures (T_a), re-

spectively. Irradiance was negligible in the dimly lighted chamber during Tests 1 and 2. Test 3 simulated the thermal conditions at unshaded nests exposed to direct solar radiation and a moderate range of air temperatures (12–24°C). Chamber air was circulated with a room fan, but air flow was not directed at the nestlings. The radiation source for Test 3 was a reflective panel of twelve 300 watt unfrosted, incandescent light bulbs which produced 1.0 to 1.2 cal/cm^2/min (as measured with a Schenk Star pyranometer) over the entire nest surface. During Test 3 the heat produced by the lights exceeded the cooling capacity of the chamber and air temperature during the 20-min test period rose approximately 11–12°C (e.g., from 12 to 24°C).

On days when two tests were performed in succession, at least 1 h was allowed for re-establishment of normal nestling body temperatures before the start of the next test. During each test run all nestlings were exposed and monitored simultaneously. During Tests 1 and 2, plastic mesh dividers prevented nestlings from huddling together. During Test 3, nestlings were permitted unrestricted movement about the nest surface. At 5-min intervals throughout the test periods, temperatures of ambient air and nestlings were measured to the nearest 0.1°C with copper-constantan thermocouples (24 ga) and a calibrated thermocouple thermometer (model TH 50, Wescor Inc., Logan, Utah). Thermocouple probes (one shielded, one unshielded) were located on the nest margin. We monitored the body temperature of each nestling with an epoxy-coated thermocouple inserted 2.5 cm through the cloaca and held in this position by a harness of plastic and leather strips (Fig. 1).

Two measures of thermoregulatory performance were calculated from the body temperature records of each nestling during each trial: (1) absolute change in nestling body temperature during the test period (ΔT_b in °C) and (2) the rate of body temperature change (i.e., slope of the least squares regression of T_b versus time, expressed as °C/min).

Age, growth, and thermoregulatory performance data were analyzed with a stepwise multiple regression to determine the measures of age and growth most correlated with the two measures of nestling thermoregulatory performance. Transformations of the five independent variables (i.e., age, body weight, tarsal length, plumage depth, and the length of the seventh primary feather) were used within a quadratic and a log model. The data for each of the three thermoregulatory tests were analyzed separately. Within each test, data from each of the two species were analyzed independently.

We measured body temperature changes in five dead nestlings (ranging in weight from 42 to 323 g) exposed to the three test conditions to assess the importance of body size and plumage on nestling thermoregulatory performance. Nestling carcasses were kept fresh by refrigeration and were tested only if they showed little dehydration (reduction in weight) or plumage alteration. Prior to each test, the body temperature of each nestling carcass was raised to a normal level (38–40°C) by placing the carcass in a warm drying oven, and then the carcass was exposed to the same three test conditions for the same lengths of time as described for live birds.

Respiration rates of randomly selected nestlings were recorded during some of the trials of Tests 1 and 3 with an impedance pneumograph and a Physiograph (E & M Instrument Co.).

RESULTS

Test 1.—The youngest nestlings of both hawk species cooled at similar rates when exposed to 16 ± 2°C. Declines in T_b were correlated with nestling age (Fig. 2). Body temperature of nestlings older than 10 to 12 days rarely decreased more than 1°C, and in some cases, nestlings older than 11 days had final body temperatures a few tenths of a degree higher

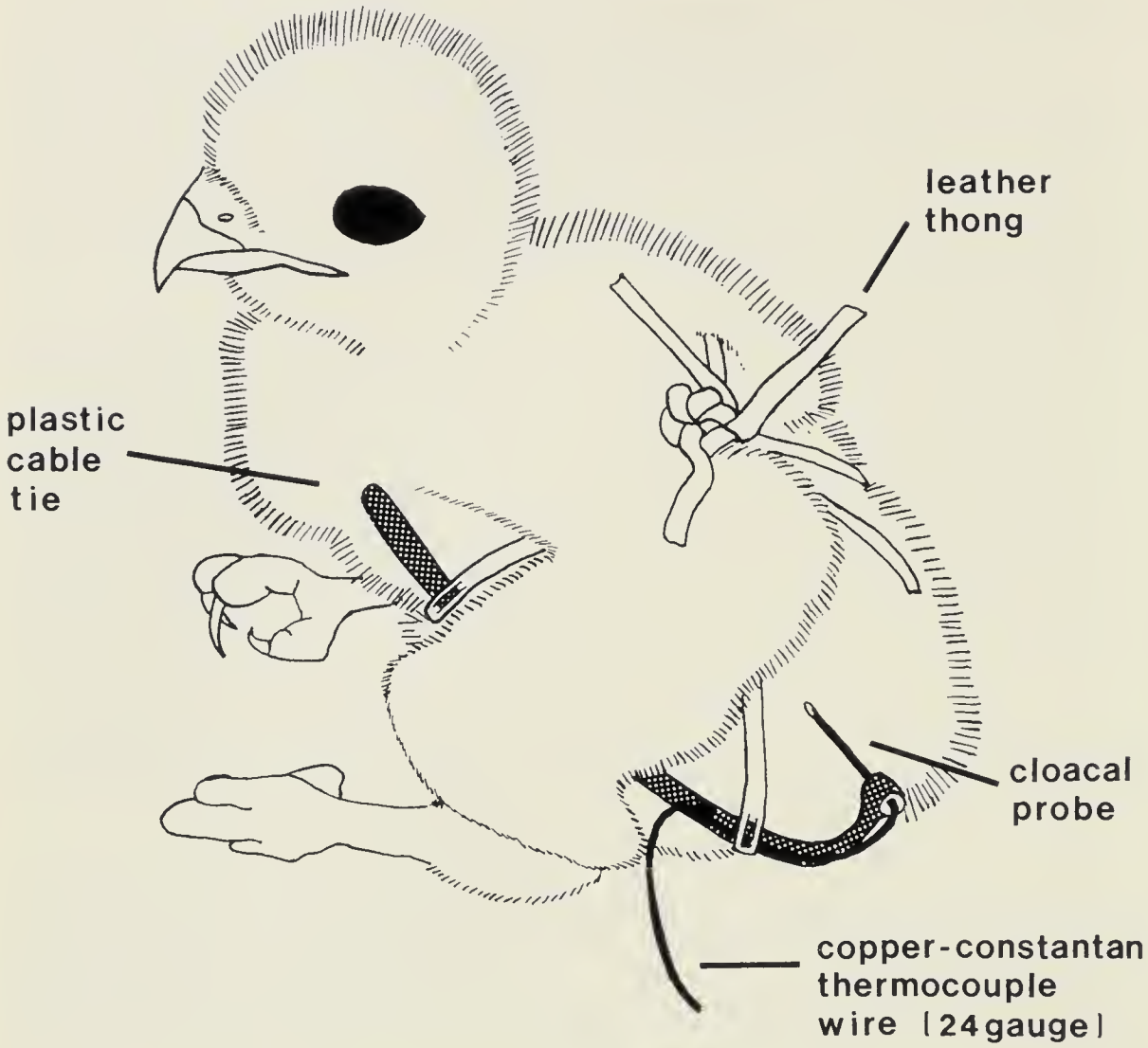

FIG. 1. Harness designed to hold thermocouple in the cloaca.

than their initial body temperatures. Age and log age were the best predictors of thermoregulatory performance for both species (Table 2). Body temperatures of the slowest growing nestling of each species frequently decreased to slightly lower levels than those of conspecifics of the same age, due, in part, to the lower pretest T_b of these runts.

Test 2.—As expected, nestling body temperatures fell more rapidly in Test 2 than in Test 1 (Fig. 2). Rate of cooling and ΔT_b were related to nestling age as in Test 1. Body temperature declines rarely exceeded 1°C in nestlings older than 13 to 15 days, and in a few instances, the body temperature of older nestlings increased over the test period. Once again, the slowest growing nestlings had slightly retarded body temperature control compared to nestlings with normal growth rates. Nestling age accounted for the highest proportion of the variability in the two dependent variables in both species when the independent variables were either

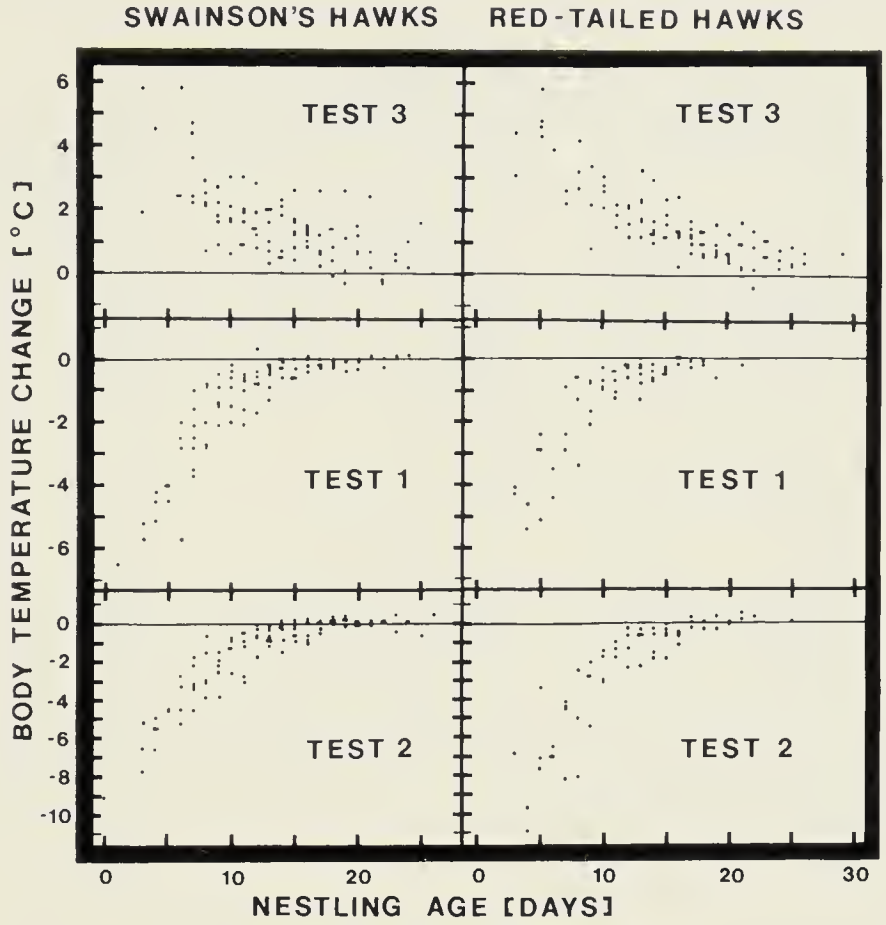

FIG. 2. Body temperature change versus age of Red-tailed Hawk and Swainson's Hawk nestlings exposed to: T_a = 16°C for 30 min (Test 1), T_a = 5°C for 30 min (Test 2), and T_a = 12 to 23°C and short wave radiation = 1 cal/cm^2/min for 20 min (Test 3).

untransformed or quadratically transformed (Table 2). When log-transformed variables were analyzed in Red-tailed Hawks, log age was the most important independent variable, whereas log body weight was the most important independent variable in Swainson's Hawks.

Heat retention improved with increasing body size of dead nestlings (Table 3). However, the body temperature decline of the largest carcass (323 g, which is a typical mass for 11–13-day-old nestlings) was about the same as that of live nestlings at 3 to 5 days of age; therefore, the improvement in nestling thermoregulation involves more than simply greater heat retention from improved feather insulation or greater body mass.

Qualitative observations of nestlings during the low temperature tests suggested that the youngest nestlings were more active in the cold than older nestlings; they struggled and vocalized as if uncomfortable or distressed. In contrast, the older nestlings lay quietly with wings and legs held close to the body and shivered visibly.

TABLE 2
SUMMARY OF THE MULTIPLE REGRESSION ANALYSES

Thermoreg. test analyzed	Model	Species[a]	Single most important independent variable[b]	Proportion of variability accounted for in the dependent variable (R^2)	
				T_b	Slope ΔT_b/time
Test 1	Quad	RT	Age	0.64	0.61
	Quad	SW	Age	0.64	0.62
	Log	RT	Log age	0.75	0.73
	Log	SW	Log age	0.80	0.78
Test 2	Quad	RT	Age	0.69	0.69
	Quad	SW	Age	0.68	0.69
	Log	RT	Log age	0.79	0.80
	Log	SW	Log body weight	0.84	0.83
Test 3	Quad	RT	Age	0.68	0.66
	Quad	SW	Tarsal length	0.39	0.34
	Log	RT	Log age	0.73	0.75
	Log	SW	Log plumage depth	0.43	0.38

[a] RT = Red-tailed hawk, SW = Swainson's hawk.
[b] Five independent variables were used; age, body weight, tarsal length, plumage depth, and length of the seventh primary feather.

For each species, respiratory frequencies at the beginning of Tests 1 and 3 and at the end of Test 1 (Table 4) were not significantly different (F-test, $P > 0.05$). Swainson's Hawk nestlings had a significantly higher average breathing rate (49.3/min) than did Red-tailed Hawks (36.4/min; t-test, $P < 0.001$).

Test 3.—The body temperatures of nestlings exposed to the irradiance and moderate temperatures of Test 3 usually increased gradually, but the final body temperature rarely exceeded 42°C. The maximum body temperature of Red-tailed Hawks was 42.3°C and of Swainson's Hawks 42.8°C (this nestling died immediately after that trial). In general, the increases in nestling body temperature rarely exceeded 3°C except for young nestlings with low initial temperatures. In a few instances the body temperatures of older nestlings decreased over the test period (Fig. 2). The apparent improvement in thermoregulatory control with age is somewhat exaggerated by the graphs for Test 3 because the initial body temperatures of young nestlings were generally a few degrees lower than those of older nestlings. Thus, some young nestlings had body temperature increases of 4 to 6°C but they did not become excessively hyperthermic (Fig. 2).

For Red-tailed Hawks age accounted for 68 and 66% of the variability in the dependent variables, ΔT_b and slope ΔT_b/time, respectively; log age

TABLE 3

SUMMARY OF BODY TEMPERATURE CHANGES OF THE CARCASSES OF RED-TAILED AND SWAINSON'S HAWK NESTLINGS EXPOSED TO THREE ENVIRONMENTAL TEST CONDITIONS (TABLE 1 DESCRIBES THE ENVIRONMENTAL CONDITIONS OF THESE TESTS)

Nestling carcasses			Average body temperature change (°C)		
Body weight (g)	Equivalent age (days)	Number of carcasses	Test 1 (N)	Test 2 (N)	Test 3 (N)
42–45	0–2	2	−11.5 (3)	−13.0 (2)	+4.4 (4)
109–120	4–6	2	−7.3 (2)	−9.9 (3)	+5.6 (3)
323	11–13	1	−7.1 (2)	−7.2 (1)	+0.7 (2)

accounted for 73 and 75% of the variability, respectively. Body temperature change and rate of body heating in Swainson's Hawks were best correlated with tarsal length and log plumage thickness, though individually, these variables accounted only for 34 to 43% of the variation in the dependent variables (Table 2). The thermoregulatory performance of individual nestlings varied from one day to the next in Test 3, thus precluding a high level of predictability using any of the independent variables. Less precise control of the ambient temperature in Test 3 resulted in greater variability in the test conditions which may also account for some of the inconsistency in nestling thermoregulatory performances. Body temperature increases within the two smallest size classes of nestling carcasses were similar to those of live nestlings of similar size, but the temperature increase of the largest carcass was less than that of live nestlings of the same size (Table 3).

One Swainson's Hawk died within minutes of the conclusion of Test 3, as mentioned previously, when its maximum body temperature had reached 42.8°C. During the same trial, the maximum body temperatures of two other Swainson's Hawks which later died were 42.6 and 41.1°C. Although neither of the latter two nestlings was subsequently exposed to the conditions of Test 3, both regurgitated food, lost weight, and died three to four days later. It is unlikely that the brief elevation of T_b of these three nestlings was the primary cause of their death. Dehydration may have been a factor in the deaths of these birds; their carcasses were about 10% lower in body water than carcasses of wild nestlings.

Regardless of age, the behavior of all nestlings during Test 3 was similar in many respects. Nestlings tended to move out from the nest center to the perimeter, their breathing rates increased, they assumed body postures characteristic of heat-stressed birds, and they showed signs of discomfort. Nestlings of all ages struggled out onto the loose sticks of the nest edge,

TABLE 4

RESPIRATION RATES OF NESTLINGS DURING THERMOREGULATORY TESTS 1 AND 3 AS DETERMINED BY AN IMPEDANCE PNEUMOGRAPH. (SEE TABLE 1 FOR ENVIRONMENTAL CONDITIONS DURING THESE TESTS)

Species	Test	Average respiration rate (breaths per minute) Initial (N)	Final (N)
Red-tailed Hawk	1	34.9 (15)	36.5 (15)
	3	37.0 (38)	176.6 (35)
Swainson's Hawk	1	46.1 (11)	48.4 (9)
	3	54.1 (9)	164.9 (9)

often selecting the same side of the nest; the direction of circulating room air may have caused a greater air flow at that location.

The time of onset of panting varied considerably. The youngest nestlings began to pant after four to six minutes of exposure, while some of the oldest nestlings panted only when exposure extended beyond the normal 20 min. Average respiration rates increased significantly (F-test, $P < 0.05$) from 37 and 54 breaths per min to 177 and 165 per minute in Red-tailed and Swainson's hawks, respectively (Table 4). Final breathing rates of these two species did not differ significantly. The maximum breathing rates we measured in Red-tailed and Swainson's hawks were 264 and 192 per min, respectively.

The typical body posture of heat stressed nestlings includes an alert, upright sitting posture with the wings either spread or loosely drooped to the sides, and with the legs held forward exposing the feet and tarsi. Nestling discomfort was suggested by high, sharp vocalizations, and frequent nervous shifting of positions on the nest. After the light panel was turned off following each trial, nestlings continued to pant for 3 to 7 min, and their body temperatures returned to normal in approximately 15 to 20 min.

DISCUSSION

Growth.—Growth rates of the captive nestlings were similar to those of the wild-reared nestlings we measured and to those of Red-tailed and Swainson's hawk nestlings studied by others (Olendorff 1971, Ricklefs 1968, Parker 1976). Some of our captive-reared nestlings grew more slowly than their conspecifics, a condition which, in wild-reared nestlings, is generally assumed to result from an unequal distribution of food to the nestlings. In contrast, all the captive nestlings were fed at frequent intervals

until satiated to insure adequate nourishment; therefore, the cause of slow growing individuals among the captive-reared nestlings is unclear. Thermoregulatory development of runt nestlings was only slightly retarded despite their slow physical growth, at times 30–50% lower than the weight of normal nestlings.

During the first 10 days of growth, nestling thermoregulation under cold conditions improved markedly (Fig. 2), but, of the four growth variables we measured, only body weight and tarsal length underwent much change. The feathers of the alar tract are practically nonexistent during this period, the first small eruptions beginning at 8–12 days of age. Before day 10, the thickness of the downy plumage remains relatively constant, and secondary down has just begun to replace primary down. This suggests to us that little, if any, of the early thermoregulatory development is due to improved insulation from the plumage.

The decrease of surface to volume ratio and increase of thermal mass during nestling growth provide greater thermal stability. Predictably, the tests on nestling carcasses showed that a larger body mass cooled less quickly in the cold and warmed more slowly under a radiation load than did a smaller body mass. However, body size cannot entirely account for the development of thermoregulation in these two hawk species since thermoregulatory development was not significantly retarded in undersized runt nestlings. Presumably, some physiological change is primarily responsible for the transition to endothermy in these hawk nestlings as suggested by O'Connor (1984).

Tolerance to hypothermia.—The responses of avian young to cold vary considerably. Nestlings of some species withstand long periods of exposure to cold, their bodies chill (T_b = 15–20°C) until they cannot move, yet when rewarmed they have no detectable adverse effects (O'Connor 1984, Dawson and Evans 1957; 1960; Dawson et al. 1972; Howell 1964). Some precocial young, although better thermoregulators than altricial young at hatching, are less tolerant to chilling at an early age; brief exposures (30 min) to moderate temperatures (20°C) can impair thermoregulatory development or cause death (Bernstein 1973, Ryser and Morrison 1954).

Red-tailed and Swainson's hawk nestlings are similar to the more cold-hardy avian species; they tolerated repeated daily exposures to the cold conditions of Tests 1 and 2. Cold-hardiness in Red-tailed Hawk nestlings was also recorded at three nests (abandoned by parental birds after placement of time-lapse cameras), where four of six nestlings survived one night of exposure, two nestlings survived two nights of exposure, and one nestling survived three nights of exposure (Kirkley 1982). Differential survival times may have been due to differences in nestling energy reserves or differences in the thermal conditions at each nest, causing different

rates of energy depletion. In hawk nests with normal parental attentiveness, nestling mortality from hypothermia is probably not a common cause of mortality, unless severe hypothermia occurs from rapid heat losses following wetting of the plumage or during strong, cold winds (Hodson 1975).

Age of endothermy.—The thermoregulatory ability of recently hatched Red-tailed and Swainson's hawk nestlings appears to be about in the middle of the graded series of thermoregulatory abilities of bird species discussed by O'Connor (1984). For instance, the 3–4°C decline in body temperature of youngest hawks after 10 min of cold exposure is comparable to the thermoregulatory abilities of some typical gallinaceous species; it is poorer than that of the precocial young of ducks but is much better than that of the altricial young of pigeons and passerines.

Dunn (1975) defined the age of endothermy in altricial birds as "that age at which nestlings can keep their body temperatures at least 75% as high above an ambient temperature of 20°C as can an adult, after some period of exposure" and she later specifies the period of exposure as "at least 20 minutes" (Dunn 1976). The nestlings we exposed to 16°C (Test 1) were endothermic at 4–5 days of age by Dunn's criteria (assuming that the body temperature of an adult hawk is 41°C). Caution should be used in applying Dunn's arbitrary definition of endothermy, however, because even our largest dead nestling (325 g) would marginally qualify as endothermic under Dunn's criteria. Dunn (1975) also indicated that the age of endothermy in 22 altricial species (adult weights ranged from 10.8 to 2050.0 g) is most highly correlated with their growth constants (K). We note that our hawk nestlings, classified as semi-altricial young, do not fit the relationship found for altricials. For example, Red-tailed and Swainson's hawk nestlings attained Dunn's age of endothermy eight to nine days earlier than would be predicted for a similarly growing altricial nestling (assuming K values of 0.161 to 0.202 as reported by Olendorff 1971 and Parker 1976).

Although Dunn's definition of the age of endothermy facilitates interspecific comparisons, its biological significance is ambiguous. Gradual and progressive endothermic development makes selecting an endpoint problematic. Tests 1 and 2 clearly showed (Fig. 2) that four- to five-day-old nestlings do not thermoregulate nearly as well as older nestlings. Body temperature control is much improved by two weeks of age, yet time-lapse films of nests show that some nestlings continue to be brooded by their parents during the third week of growth, especially overnight (Kirkley 1982). Therefore, we concur with O'Connor's (1984) statement that in some cases "the extent of parental brooding is probably the best available guide to the thermoregulatory abilities of the young" under the prevailing conditions.

Nestling behavioral strategies for coping with cold appear to change with nestling age. Hawk nestlings that are too young to thermoregulate effectively tend to vocalize and struggle, which presumably would increase their chances of locating and huddling with siblings or of eliciting parental brooding behavior. Nestlings more capable of shivering thermogenesis tend to lie motionless with the extremities held close to the body, thus conserving heat. Similar age-related changes in the behavior of cold-stressed nestlings have been observed in other species such as Willow Ptarmigan (*Lagopus lagopus*) (Aulie 1976). We observed with time-lapse films and visits to nests that young hawks often huddled together in the nest depression during adult absences, especially when ambient temperatures were low. Dunn (1976, 1979) emphasized the advantage of this means of heat conservation by showing that larger broods of altricial nestlings attain "effective" endothermy at an earlier age than do smaller broods and at a considerably earlier age than predicted from the "physiological" age of endothermy in isolated nestlings.

Tolerance to hyperthermia.—Overheating in avian young is probably more prevalent among species that build nests exposed to direct insolation in hot, arid climates, but hyperthermia can also occur in protected nests such as cavities occupied by many nestlings (Mertens 1977). Beecham and Kochert (1975) report that heat prostration possibly caused 41 percent of the nestling mortality in Golden Eagles (*Aquila chrysaetos*) in southwestern Idaho. Mosher and White (1976) suggest that Golden Eagles may preferentially select nest sites which minimize thermally stressful conditions, a conclusion questioned by Collopy (1980).

Strategies for coping with heat stress involve both behavioral and physiological mechanisms. The restless movements of nestlings of all ages shortly after the illumination of the light panel (Test 3) may have helped them find a place with better convection. In the wild, these movements may also help nestlings locate shaded places on the nest surface or may stimulate a parent to begin shading. When adults and shade are absent, heat-stressed nestlings often climb out onto the nest margin; the slightly elevated position and loose arrangement of the sticks presumably facilitate nestling heat loss through convection. The spread posture of nestlings during heat stress also enhances heat dissipation by exposing the unfeathered areas beneath the wings and on the feet and tarsi. Feet and legs are reported to be important heat dissipating structures in raptors (Bartholomew and Cade 1957, Mosher and White 1978) and in other birds (Howell and Bartholomew 1961, 1962; Kahl 1963; Bartholomew 1966). The importance of the legs in thermoregulation may account for tarsal length as one of the more important predictors of thermoregulatory performance in Test 3.

Panting (or gular flutter in some species) increases the rate of evapo-

rative water loss from the respiratory surfaces and is a primary mechanism for augmenting heat loss in birds (Kirkley 1985). Nestlings in Test 3 began to breathe with their mouths open before their body temperatures had risen more than 1 or 2°C. By the end of 20 min, average breathing rates were 3–5 times that of normal. During panting the beak is opened fully, the tongue is lifted forward from the lower mandible, and the surfaces of the mouth are kept moist with mucus which occasionally drips from the tongue and lower mandible. The tendency in Test 3 for T_b to increase slightly in nestlings of all ages suggests that heat-stressed hawk nestlings may, like other birds (O'Connor 1984), employ adaptive hyperthermia rather than maintaining a normal T_b.

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FRESHWATER WETLANDS, RAINFALL, AND THE BREEDING ECOLOGY OF WHITE IBISES IN COASTAL SOUTH CAROLINA

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ABSTRACT.—The numbers of White Ibises (*Eudocimus albus*) nesting on Drum Island in the Cooper River and on Pumpkinseed Island in Winyah Bay, the two largest wading bird colonies along the South Carolina coast, declined from over 12,000 pairs at each site in a very wet year (1984) to less than 2000 pairs at each site in 1985, one of the driest springs on record. The following year, when the area around Pumpkinseed Island received slightly above average rainfall, but the area around Drum Island received slightly below average rainfall, the number of pairs breeding at Pumpkinseed increased to 5132, while the number of pairs at Drum decreased to 388. On Drum Island, the percent of ibis eggs that resulted in fledgings declined from 39% in 1984 to 3% in 1985. Other more piscivorous wading birds breeding on Drum Island did not exhibit similar declines in numbers or in reproductive success in 1985. On Pumpkinseed Island a substantially lower proportion of ibises flew inland to feed on crayfishes in freshwater wetlands in 1985 and 1986 than in 1984. At both sites, nestling diets contained a lower proportion of crayfish in 1985 than in 1984, and many more nestlings starved or were abandoned by their parents in 1985, and to a lesser extent in 1986, than in 1984.

We suggest that declines in both the numbers of nesting ibises and in reproductive success at the two sites resulted from the relative unavailability of crayfishes during dry periods. At Drum Island, mortality associated with food stress was exacerbated by Fish Crow (*Corvus ossifragus*) predation on eggs and young. Although alternative prey such as fiddler crabs are consumed by adult ibises, the osmotic concentration of these prey results in unacceptable salt loading in developing nestlings. White Ibises breeding in salt marshes along the South Carolina coast appear to depend heavily upon freshwater wetlands as a source of food for their nestlings. *Received 8 Nov. 1988, accepted 10 March 1989.*

White Ibises (*Eudocimus albus*) are long-legged, tactilely foraging wading birds (Kushlan 1978) that feed mainly on crustaceans, aquatic insects, and fishes (Nesbitt et al. 1974, Kushlan and Kushlan 1975). Although White Ibises were first reported breeding in South Carolina only in 1922 (Wayne 1922), the number of ibises along the South Carolina coast has long been linked with rainfall (Catesby 1731–43). More recently, researchers have suggested that reproductive effort in White Ibises, as well as in at least 10 other species of ibises (Threskiornithidae) (Table 1), is affected

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TABLE 1

SPECIES OF IBISES IN WHICH REPRODUCTIVE EFFORT IS REPORTED TO BE AFFECTED BY SEASONAL VARIATION IN RAINFALL AND SUBSEQUENT CHANGES IN FOOD AVAILABILITY

Species	Source
Sacred Ibis (*Threskiornis aethiopica*)	(Urban 1974)
Australian White Ibis (*T. molucca*)	(Carrick 1962)
Straw-necked Ibis (*T. spinicollis*)	(Carrick 1962, Waterman et al. 1971)
Waldrapp (*Geronticus eremita*)	(Robin 1973)
Bald Ibis (*G. calvus*)	(Manry 1985a)
Green Ibis (*Mesembinibis cayennensis*)	(Thomas 1979, Luthin 1983)
Whispering Ibis (*Phimosus infuscatus*)	(Thomas 1979, Luthin 1983)
White Ibis (*Eudocimus albus*)	(Dusi and Dusi 1968; Kushlan 1976, 1979; Ogden et al. 1980)
Scarlet Ibis (*E. ruber*)	(ffrench and Haverschmidt 1970, Thomas 1979, Luthin 1983)
Glossy Ibis (*Plegadis falcinellus*)	(Carrick 1962)
White-faced Ibis (*P. chihi*)	(Ryder 1967)

by variation in seasonal rainfall because of subsequent changes in the availability of prey. Here we: (1) compare the feeding ecology and reproductive success of White Ibises at the two largest coastal colonies in South Carolina during wet and dry years, (2) describe a causal link between rainfall and ibis reproductive success, and (3) discuss the importance of freshwater wetlands and crayfishes in the breeding ecology of this species.

METHODS

Study areas.—Coastal South Carolina, which experiences a mild maritime climate, receives an average of 110–130 cm of rain annually. The driest season, which typically occurs in October–November, is followed by increasing rainfall that peaks in March, and by a second wet period from June through early September (Barry 1980).

We studied White Ibises in coastal South Carolina during the breeding seasons of 1978–1986 on Pumpkinseed Island in Winyah Bay near Georgetown, South Carolina (K.L.B., J.J., P.F.); and during the breeding seasons of 1984–1986 on Drum Island, in the Cooper River, Charleston, South Carolina (W.P.) (Fig. 1). The two sites, which are 85 km apart, together with a single, recently established, large colony in coastal North Carolina 140 km to the northeast of Pumpkinseed Island (Shields and Parnell 1986), represent the three northernmost large colonies (>1000 pairs) of the Atlantic Coast population of White Ibises (Osborn and Custer 1978).

Pumpkinseed Island is a 9-ha marsh island in Winyah Bay. The island, which is regularly inundated by high tides, is vegetated with a dense stand of mostly black needle rush (*Juncus roemerianus*), along with some big cord grass (*Spartina cynosuroides*) and smooth cord grass (*S. alterniflora*) in low-lying areas. A narrow strip of marsh elder (*Iva frutescens*) occurs along the northeastern edge of the island. Although a few ibises may nest in marsh elder along with Great Egrets (*Casmerodius albus*) and Black-crowned Night-Herons (*Nycticorax nycticorax*), most nest on matted-down clumps of black needle rush (Frederick 1985) along

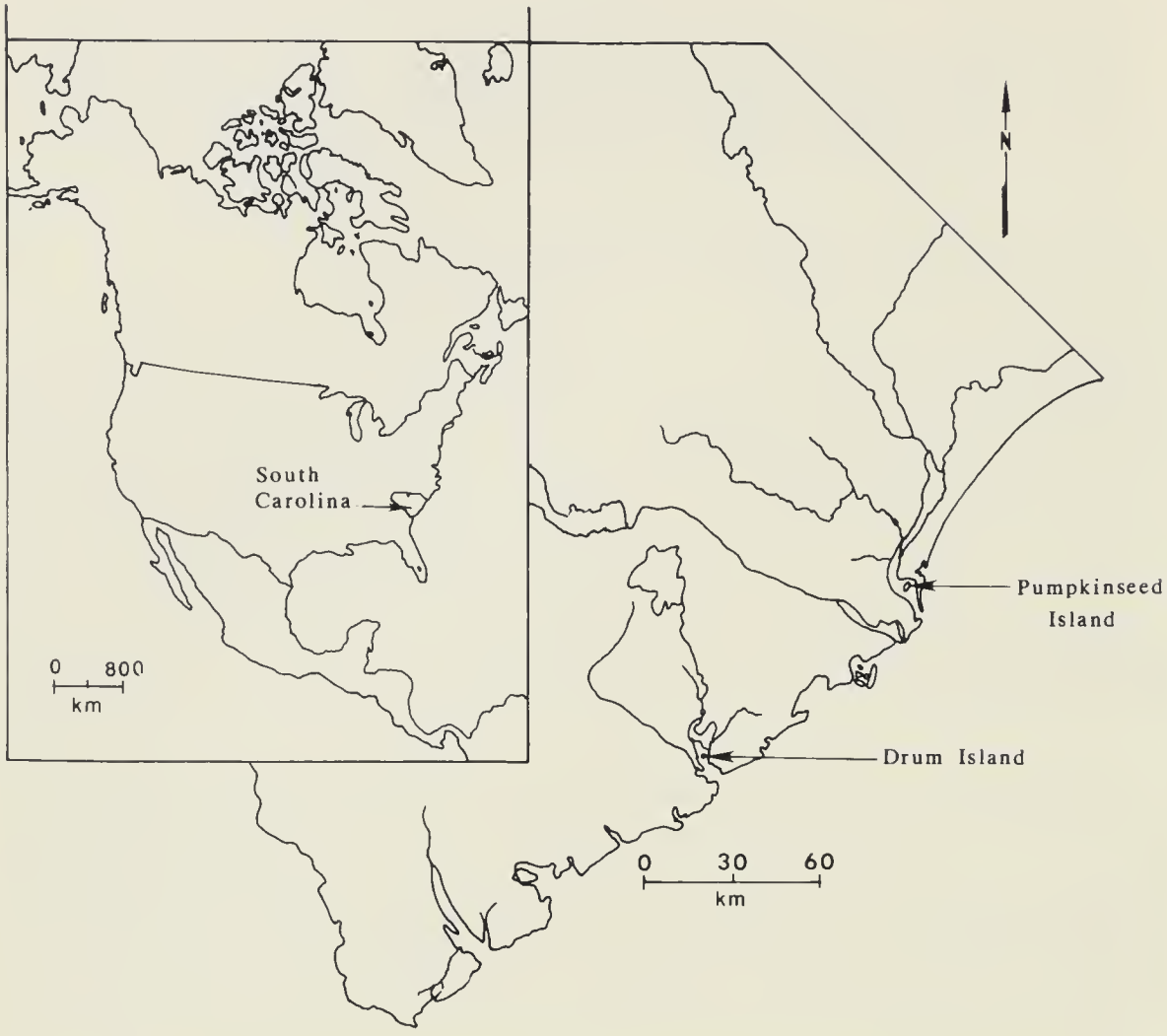

FIG. 1. Location of Pumpkinseed and Drum islands in coastal South Carolina.

with Glossy Ibises (*Plegadis falcinellus*), Little Blue Herons (*Egretta caerula*), and Tricolored Herons (*E. tricolor*). White Ibises have nested on Pumpkinseed Island at least since 1967 (Frederick, unpubl. data).

Drum Island is a 75-ha dredge-spoil island in the lower Cooper River within 3 km of downtown Charleston, South Carolina. The island is vegetated with white mulberry (*Morus alba*), hackberry (*Celtis* sp.), and groundsel (*Baccharis* spp.). Most ibis nests are in a 10-ha stand of mulberry at the southern end of the island among lesser numbers of nesting Great Egrets, Snowy Egrets (*E. thula*), Little Blue Herons, Tricolored Herons, Cattle Egrets (*Bubulcus ibis*), Green-backed Herons (*Butorides striatus*), Black-crowned Night-Herons, Yellow-crowned Night-Herons (*N. violaceus*), and Glossy Ibises. Ibises have nested on Drum Island since 1957 (The Charleston Museum, unpubl. data). Although White Ibises are usually the most numerous species of wading birds at both sites, at least seven other Ciconiiforms nest on Pumpkinseed Island (Bildstein et al. 1982), and at least nine other Ciconiiforms nest on Drum Island (Post, unpubl. data).

Population estimates and reproductive success.—We censused ibis nests on Pumpkinseed Island from fixed-wing aircraft flying at approximately 150 m during a series of counts timed to document peak numbers of nests and to assess the effects of extreme high tides on the survivorship of eggs and young nestlings (Frederick 1987). Flights were made on 5 June

1979, 12 May 1980, 28 April 1981, 5 May and 15 June 1982, 13 April 1983, 14 May 1984, 4 May 1985, and 8 May 1986. Comparisons of aerial counts with ground counts of marked quadrats indicate >95% accuracy of the acrial counts (De Coursey, pers. comm.)

We censused wading bird nests on Drum Island from the ground. In addition to counting nesting White Ibises, we also counted nesting Great Egrets, Snowy Egrets, Little Blue Herons, Tricolored Herons, Cattle Egrets, Green-backed Herons, Black-crowned Night-Herons, Yellow-crowned Night-Herons, and Glossy Ibises. In 1984 the census involved extrapolation from a 6-m × 395-m (0.237-ha) transect. In 1985 the census was based on 115 100-m^2 (1.2 ha total) randomly chosen plots. In 1986 the estimate was based on 110 100-m^2 plots (1.1 ha). To estimate nesting success of birds on Drum Island, we visited the site weekly and marked each active nest with a numbered flag. Flagged nests were considered successful when young reached the age at which they were able to climb into the canopy.

Nestling diet.—At Pumpkinseed Island we collected disgorged regurgitant, by throat massage when necessary, from 8- to 24-day-old nestlings in late June–early July 1984, late May and late June–early July 1985, and late May and mid–July 1986. We immediately estimated the percent by volume of fiddler crabs (*Uca* spp.), crayfish (*Procambarus* spp.), fish, insects, and other invertebrate prey in each sample. On Drum Island regurgitant was fixed in 10% formalin in the field and then transferred to 70% ethanol for later analysis.

Foraging ecology.—Numbers of ibises feeding on fiddler crabs on the Bly Creek Drainage (cf. Bildstein 1983), a portion of the North Inlet salt marsh approximately 6 km from Pumpkinseed Island, were recorded during dawn-to-dusk observations collected over 7- to 10-day intervals during May–August 1984 (N = 15), March–July 1985 (N = 11), and March–August 1986 (N = 15). Concurrently, the numbers of ibises flying over the same salt marsh enroute to more distant freshwater swamps 10–40 km from the colony site (determined by following several flocks in a fixed-wing aircraft) were counted from dawn-to-dusk during "composite days" over the same 7- to 10-day intervals. (Each composite day consisted of a series of 2–4-h nonoverlapping watches conducted during all times between dawn and dusk over the course of a 7- to 10-day period.)

Rainfall.—Monthly rainfall data from North Charleston (15 km from Drum Island) for July 1983 through June 1986, and from Georgetown (13 km from Pumpkinseed Island) for July 1978 through June 1986 were compared with monthly, 30-year means collected at the two sites (U.S.D.C. 1974–1986). Variation in the amount of winter–spring rainfall at Georgetown, where it has been studied in some detail, is positively correlated with the degree of flooding in bottomland forest swamps used by foraging ibises nesting at nearby Pumpkinseed Island (E. Blood pers. comm.). This same rclationship between rainfall and flooding appears to hold for the area around the Drum Island colony site.

RESULTS

Nesting populations.—The numbers of White Ibises nesting on Pumpkinseed Island were relatively constant during the first four years of the study, when between 6000 and 8000 pairs bred on the island. The number of nesting pairs increased in 1983 and again in 1984, when almost 13,000 pairs bred on the island, before decreasing in 1985 by 85% to less than 2000 pairs. The decline in the number of nesting birds occurred despite the fact that the numbers of ibises returning to the area in late March and early April were similar in 1984 and 1985. In 1986 more than 5000 pairs again bred on the island (Table 2). Similarly, although over 13,000 pairs of ibises bred on Drum Island in 1984, the number of birds nesting on

TABLE 2

NUMBERS OF WHITE IBISES NESTING ON PUMPKINSEED ISLAND NEAR GEORGETOWN, SOUTH CAROLINA, 1979–1986, AND ON DRUM ISLAND NEAR CHARLESTON, SOUTH CAROLINA, 1984–1986

	Numbers of breeding pairs							
	1979	1980	1981	1982	1983	1984	1985	1986
Pumpkinseed Island	7933	6669[a]	7887	7814	10,035	12,973	1976	5132
Drum Island	NC[b]	NC	NC	NC	NC	13,763	949	388

[a] Pumpkinseed Island colony sizes for 1980–1984 are from Frederick 1987.
[b] No count.

the island decreased in 1985 by 95% to fewer than 1000 pairs. A further decline to 388 pairs occurred in 1986 (Table 2). The numbers of herons and egrets that were recorded nesting on Drum Island in 1984 and 1985 failed to show a similar catastrophic decline (Table 3).

Reproductive success.—On Pumpkinseed Island, where White Ibises nested near the ground in black needle rush, mortality during the egg stage usually resulted from tidal inundations (Frederick 1987). In 1984, for example, an estimated 42% of the nests were flooded by high tides during the egg and early nestling stages on 16–17 May (Frederick 1987). In 1985 50% of the nests were lost during the egg stage to high tides on 5 May. Similarly, exceptionally high tides between 18 and 24 May 1986 caused the death of 16 of 30 3–15-day-old young whose growth we were monitoring. In 1984 avian predation, probably by Fish Crows, accounted for the loss of 8% (N = 468) of ibis eggs (Frederick 1987). Although nestling losses to avian predators were not studied in detail on Pumpkinseed Island, Black-crowned Night-Herons were seen taking small nestlings in

TABLE 3

NUMBERS OF OTHER SPECIES OF HERONS AND EGRETS NESTING ON DRUM ISLAND 1984–1985

Species	Numbers of breeding pairs		% deviation from 1984
	1984	1985	
Small white herons[a]	2209	1628	−26%
Great Egret	797	779	−2%
Tricolored Heron	720	934	+30%
Black-crowned Night-Heron	683	524	−30%
All species combined	4409	3865	−12%

[a] Small white herons include Little Blue Herons, Cattle Egrets, and Snowy Egrets.

TABLE 4
REPRODUCTIVE SUCCESS OF HERONS AND EGRETS BREEDING ON DRUM ISLAND 1984–1985

	Percent of eggs producing fledglings[a]				
	1984		1985		% change from 1984
	N	%	N	%	
Great Egret	20 (7)[b]	80%	99 (42)	57%	−29%
Tricolored Heron	54 (18)	44%	149 (50)	60%	+36%
Black-crowned Night-Heron	35 (12)	40%	100 (34)	40%	0%
White Ibis	390 (158)	39%	347 (166)	3%	−92%

[a] Young that were capable of climbing out of nests. (Great Egret nestlings were able to do this at 26 days-of-age, Tricolored Herons at 24 days-of-age, and White Ibises and Black-crowned Night-Herons at 21 days-of-age.)
[b] Number of eggs (number of nests).

1984, 1985, and 1986. The extent of this predation is unknown, but observations indicated that it was limited to very small young (Frederick 1985, see also Rudegeair 1975), and that it was not substantial (i.e., <10%). Starved, desiccated, and seemingly abandoned nestlings up to 30 days old were quite common in 1985, especially in June and July among late nesters. Although a few starved young were seen in 1986, again mainly among late nesters, none were seen in 1984.

On Drum Island, where ibises nested in white mulberry and thus were not subject to tidal inundation, egg predation by Fish Crows was the only significant source of egg mortality. In 1985 and 1986 68% and 96%, respectively, of egg losses were attributed to predators. As was the case on Pumpkinseed Island, dozens of starved, desiccated ibises were seen on Drum Island in 1985, but not in 1984. As a result of the combined effects of avian predation and apparent adult abandonment, 39% of 390 eggs monitored in 1984, but only 3% of 347 eggs monitored in 1985 produced fledged young. There were no similar declines in the reproductive success of herons and egrets breeding on the island (Table 4).

Adult foraging behavior.—At Pumpkinseed Island the peak number of ibises flying inland to feed in freshwater swamps was higher in 1984 than in either 1985 or 1986 (Fig. 2). In 1984 large numbers of adult ibises continued flying to and from freshwater swamps through June and into July. In 1985 the numbers of ibises flying inland to freshwater swamps declined sharply in early May; and in 1986 the decline occurred in late May (Fig. 2). In all three years, declines in the numbers of birds flying inland were accompanied by simultaneous increases in the numbers of birds feeding in a salt marsh 6 km north of the colony site (Fig. 2).

Nestling diets.—On Pumpkinseed Island, although nestlings were still being fed large numbers of freshwater crayfishes in late June–early July

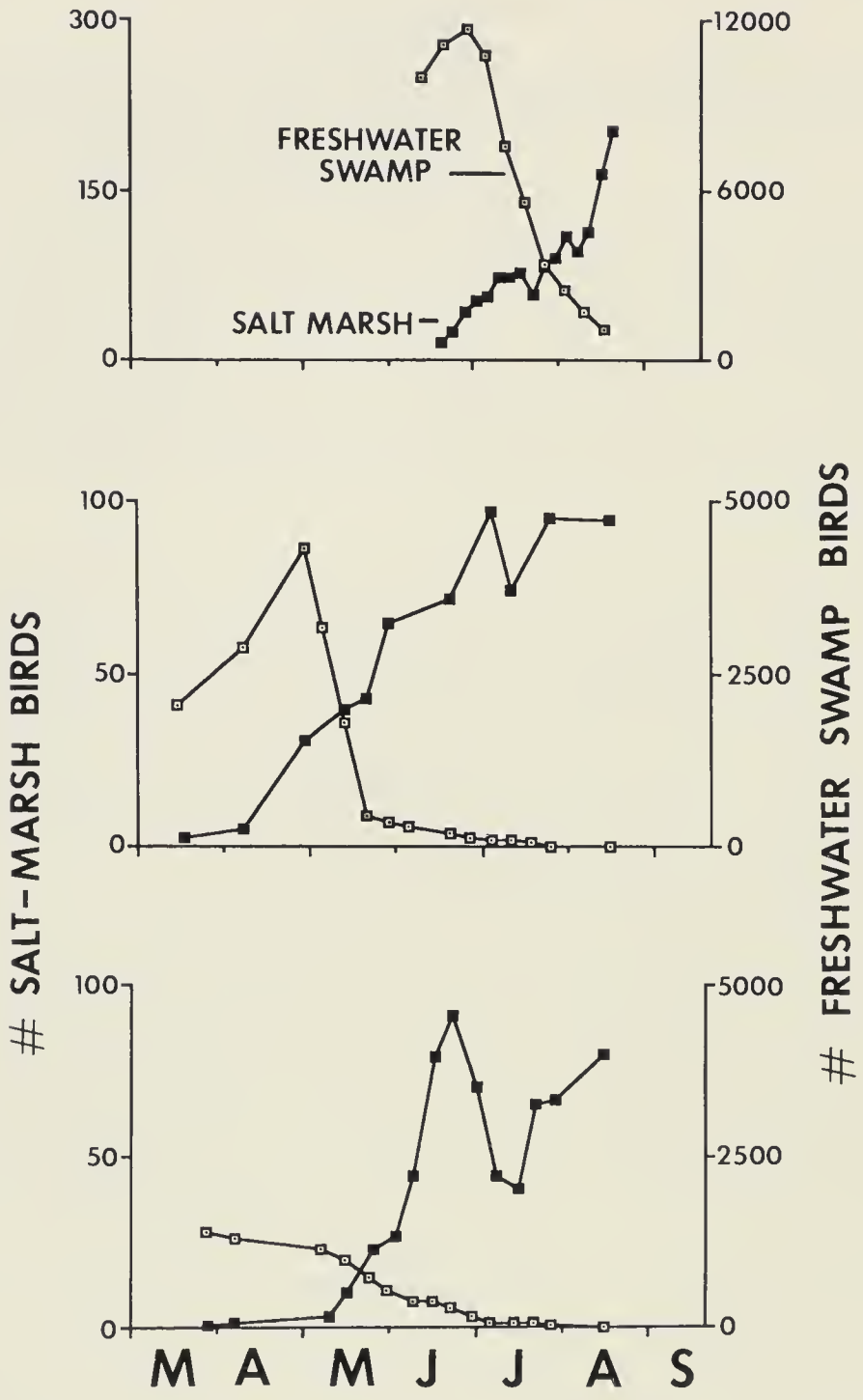

FIG. 2. Three-week running means of the numbers of adult ibises seen: (1) flying inland to feed in distant freshwater swamps, and (2) feeding on a nearby saltwater marsh. Freshwater swamp counts represent the total number of adult ibises seen on composite days of observations collected weekly between March and August. (See Methods section for definition of composite day.) Salt-marsh counts are based on the mean number of adult ibises seen feeding on the 65-ha salt-marsh site during single days of dawn-to-dusk hourly counts.

TABLE 5

PERCENT BY VOLUME OF PREY IN REGURGITANT TAKEN FROM 8- TO 24-DAY-OLD WHITE IBIS NESTLINGS ON PUMPKINSEED ISLAND IN 1984, 1985, AND 1986

		1985		1986	
	1984 (N = 28)	Early (N = 23)	Late (N = 32)	Early (N = 35)	Late (N = 36)
Collection dates	28 June–3 July	23–29 May	12 June–6 July	11–26 May	13–20 July
Prey					
Crayfish	85	39	1	81	0
Fiddler crabs	2	44	82	8	20
Fishes	5	7	11	5	45
Insects	5	6	3	1	17
Other invertebrates	3	6	2	6	18

1984, crayfishes were not a significant portion of the diet late in the breeding season in either 1985 or 1986 (Table 5). In 1985 ibises switched from feeding crayfishes to their nestlings to feeding mainly fiddler crabs. In 1986 ibises switched from crayfishes to fishes, and, to a lesser extent, to fiddler crabs and insects (Table 5). On Drum Island, in 1985 crayfishes made up only 20%, by number, of the diet (N = 22). The majority of the diet was grass shrimp (*Palaemonetes* sp.) and mud crabs (*Sesarma* sp.), both of which are found in brackish water.

Rainfall.—Total rainfall during the six months preceding the start of hatching (approximated as 1 May) at both sites was substantially above the 30-year mean in 1984, and substantially below the mean in 1985. In 1986 rainfall during the same period near Pumpkinseed Island was slightly above the 30-year mean, whereas near Drum Island it was slightly below the mean (Table 6). Regression analysis of rainfall and colony size at Pumpkinseed Island during the 8-year period from 1978 to 1986 revealed: (1) that more ibises nested in wet years than in dry years, and (2) that variation in rainfall during the 6-month period preceding hatching explained 71% of the annual variation in the maximum number of ibises nesting at the site ($P < 0.05$) (Fig. 3).

DISCUSSION

Although the proximate reasons differ among species, rainfall ultimately affects the breeding biology of a number of species of ibis (Table 1). Manry (1982, 1985a, b) has linked declines in the numbers of breeding Bald Ibises (scientific names are in Table 1) in southern Africa to reduced

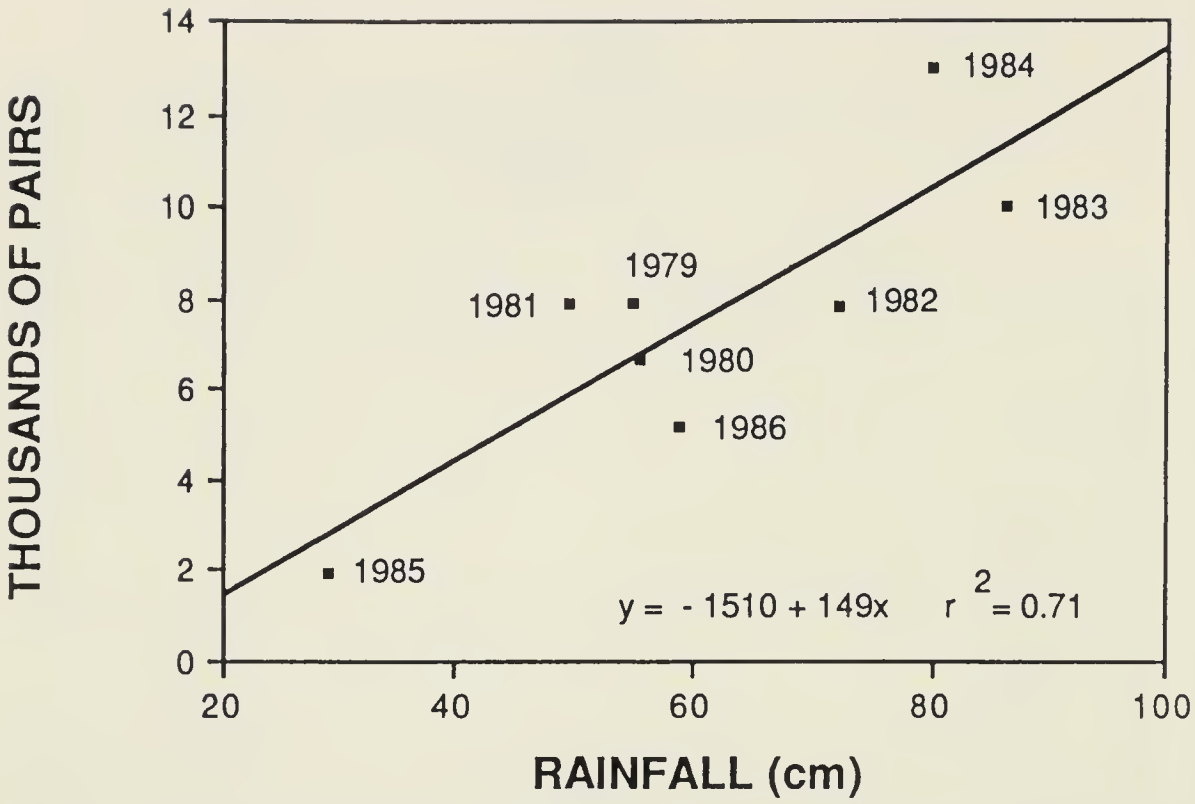

FIG. 3. Linear regression analysis depicting the relationship between the numbers of pairs of ibises breeding on Pumpkinseed Island and the amount of rainfall at Georgetown, South Carolina, during the six-month period (November–April) preceding the initiation of hatching at the colony site. (The relationship is significant at $P < 0.05$.)

grazing and grassland burning during drought years which, in turn, reduced the availability of essential insect prey. Individuals that did breed during dry years laid smaller clutches and were more likely to desert their nests and allow their chicks to starve (Manry 1985a). Similar reductions in the numbers of Waldrapps breeding in Morocco have been reported by Robin (1973). In Ethiopia and South Africa, Sacred Ibises breed only after the onset of the rainy season. However, it is not clear whether they do so in response to increased food availability, or because of reduced predation pressure (Urban 1974, Clark and Clark 1979). In Australia, Straw-necked, Australian White, and Glossy ibises are nomadic breeders that restrict their reproductive attempts to sites experiencing heavy flooding rains (Carrick 1962, Waterman et al. 1971, Woodall 1985), presumably because of their dependence on aquatic food sources (Carrick 1959). In western North America, White-faced Ibises shift breeding locations in response to rainfall patterns and often fail to nest in drought years (Ryder 1967). Luthin (1983) reports a similar response in Whispering, Green, and Scarlet ibises to flooding rains in the llanos of Venezuela. Scarlet

TABLE 6

PERCENT DEVIATION FROM 30-YEAR MEAN IN RAINFALL AT GEORGETOWN AND CHARLESTON, SOUTH CAROLINA, DURING THE 6- AND 12-MONTH PERIODS PRECEDING THE 1984–1986 HATCHING PERIODS FOR WHITE IBISES

Breeding season	Number of months preceding the initiation of hatching[a]	Percent deviation in rainfall from 30-year mean[b]	
		Georgetown	Charleston
1984	6	+62	+48
	12	+4	−5
1985	6	−41	−56
	12	−10	−38
1986	6	+20	−13
	12	+14	+4

[a] The initiation of hatching is approximated as 1 May in each of the three years.
[b] Data are from the U.S. Department of Commerce weather stations at Georgetown and Charleston, South Carolina.

Ibises also restrict their breeding to rainy periods in Surinam and Trinidad (Snow and Snow 1964, ffrench and Haverschmidt 1970).

For White Ibises, Kushlan (1976) reports a similar response to rainfall for populations in South Florida, where the number of breeding birds was 35 times greater in a wet year than it had been in the previous drought year. Because most White Ibises breeding in Florida feed near water, usually along the edges of flooded areas to a depth of about 25 cm, Kushlan (1979) attributed the dramatic shift in the numbers of breeding birds to the lack of a sufficient receding line of shallow aquatic habitat during the drought. That the only successful breeders during the drought were in the smaller coastal colonies in tidally inundated areas supports this notion. Similar reports of White Ibises feeding along the receding or advancing edges of flooded pastures (Bateman 1970), clearcuts (Stinner 1983), and rice fields used as breeding sites for crayfishes (Martin and Hamilton 1985) strengthen the argument that water depth is extremely important to White Ibises feeding in aquatic habitats. Our data indicate that the same situation holds for White Ibises breeding in coastal South Carolina. During each breeding season we saw large numbers of ibises flying long distances (in some instances 40 km one-way) inland to secure crayfishes from flooded bottomland hardwood forests (Fig. 2), where crayfishes tend to concentrate along the rising and falling water's edge in spring during periods of inundation of this habitat (cf. Pollard et al. 1982). In drought years, such as 1985 and 1986, when there is little or no inundation of these bottomland flood-plains, the little shallow aquatic habitat available dries out earlier

in the season, and crayfishes burrow into the substrate (cf. Pollard et al. 1982) and are no longer readily available to ibises (cf. Audubon 1840–1844). In response to this loss of a prey base, those ibises that do breed during the drought must turn to alternative sources of food, including fishes, fiddler crabs, insects, and other invertebrates (Table 5).

White Ibises are primarily tactile foragers in aquatic habitats (Kushlan 1977), and their probing behavior in such situations is apparently "effective for catching crayfishes but not fish," except in unusual circumstances (Kushlan 1979). With the exception of fiddler crabs, other invertebrates apparently are not available in densities sufficient to support large numbers of breeding ibises. Although fiddler crabs are readily abundant near both of the coastal colonies we studied, and although they are taken by some ibises throughout the breeding season (Bildstein 1983, 1984), they do not appear to be used heavily by parental ibises as food for their nestlings as long as crayfish are available (Table 5, Fig. 2). Indeed, our data together with those collected by researchers in Florida (Ogden et al. 1980, Kushlan 1979) indicate that unless crayfish comprise the bulk of the nestling's diet, large numbers of ibises will not breed successfully, even in areas with an abundance of fiddler crabs. Although in coastal South Carolina crayfishes have a substantially higher caloric content than do fiddler crabs (4.1 kcal/g versus 2.3 kcal/g; see also Kushlan 1979, Shanholtzer 1973), the latter are more readily available closer to both colony sites, and they are caught by the few ibises that do feed upon them during the nestling period at rates that should permit parental ibises to meet the caloric requirements of their developing young (cf. Bildstein 1987). Yet in spite of the availability of fiddler crabs within 5–10 km of both sites, most individuals breeding at Pumpkinseed Island—where flight paths to feeding areas were followed closely in 1984, 1985, and 1986 (Fig. 2)—flew up to 40 km inland to feed on crayfishes, as long as this prey was available each season. (See Pennycuick and De Santo [1989] for estimates of flight speeds and energetic costs incurred during such flights.)

Fiddler crabs are osmotic conformers, and because they inhabit salt marshes, are saltier than are freshwater crayfishes (800–1100 mOSM versus 500–600 mOSM). Salt glands are prominent features above the orbits of 10–12-day-old white ibis embryos, and nestling ibises possess functional salt glands at least by the time they are 20 days old. However, captive-reared 20- to 25-day-old nestlings fed a diet of either fiddler crabs or crayfishes spiked to the osmotic concentration of fiddler crabs survived and developed only if fresh water was available as a supplement to these salty diets (Johnston and Bildstein 1990). As fresh water is not normally available to nestlings at either colony site, and as there is no indication that adults bring fresh water to the young, fiddler crabs do not appear to

be physiologically available as a food source for nestling ibises. Recently fledged, free-flying juveniles, as well as adult ibises, readily consume fiddler crabs in coastal South Carolina (Wayne 1922, Bildstein 1983), apparently because they are able to secure the necessary fresh water needed to dilute the osmotic concentration of their prey.

During the especially dry breeding season of 1985 (Table 6), the relative amount of crayfish prey in the diet of nestling ibises declined early in the season (Table 5), presumably as a result of the earlier drying-out of inland bottomland hardwood forest flood-plains. In that year, many of the adult ibises that returned to both Drum Island and Pumpkinseed Island in March did not breed (Table 2) and, at least at Pumpkinseed Island, those that did breed fed their nestlings fiddler crabs (Table 5). Nestlings from which we recovered predominantly fiddler crab prey were usually lethargic, and several were moribund. Parental care at both colonies seemed to wane, perhaps as a result of this type of nestling behavior, and at both colonies parent ibises abandoned large numbers of young in 1985. At Pumpkinseed Island these young, many of which were ambulatory, wandered from the vicinity of their nests before they were capable of feeding on their own and then starved. At Drum Island, many recently abandoned young were preyed upon by Fish Crows (Table 4) whose populations were quite high, apparently as a result of the recent establishment of a nearby garbage dump. Dusi and Dusi (1968), reporting a similar drought-related increase in Fish Crow predation at a wading bird colony in Alabama, also attributed the increased predation to the abandonment of nestlings by adults unable to secure sufficient prey for their young. In 1986 when spring rainfall was near normal at Pumpkinseed Island, but still somewhat below normal at Drum Island (Table 6), the numbers of breeding ibises rebounded at Pumpkinseed Island but continued to decline at Drum Island (Table 2). Nestlings at Pumpkinseed Island fared better in 1986 than in 1985. In both years, parent ibises switched from crayfishes to alternative prey during the nestling season (Table 5), but in 1986 alternative prey included a greater amount of osmotically benign items such as fishes (Table 5). Similarly, we suggest that a relatively greater dependence upon fish prey (Post unpubl. data) enabled most other species of wading birds nesting at Drum Island to breed successfully in 1985 (Table 4).

Even in coastal areas, where White Ibis populations typically are more stable than they are inland (Kushlan 1976), rainfall—by inducing shifts in prey availability—has a dramatic effect on the breeding success of the species. During droughts in coastal South Carolina, ibises nesting in tidal areas respond to low rainfall not because of drought-induced fluctuations in prey availability in the immediate vicinity of the nest but because low

rainfall reduces the availability of essential freshwater prey in more distant inland bottomland swamps.

In Trinidad, where Scarlet Ibises roost and sometimes nest in coastal mangrove swamps, nonbreeding individuals typically feed on brackish-water prey such as crabs and polychaete worms (ffrench and Haverschmidt 1970, Bildstein unpubl. data). During the breeding season, however, parent ibises fly inland from their coastal colony sites to collect freshwater prey for their young (ffrench and Haverschmidt 1970). These observations, together with the possibility that Scarlet and White ibises may be color morphs of the same species (Ramo and Busto 1987), suggest that Scarlet Ibises too are physiologically constrained in their choice of prey for developing young. Wildlife managers and conservationists interested in maintaining populations, as well as in reversing recent declines in the numbers of Scarlet Ibises should consider acquiring sufficient acreage of inland wetlands, as well as coastal habitat, to support this species.

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TEMPORAL VARIATION IN MICROHABITAT RELATIONSHIPS AMONG GREBES AND COOTS

GREGORY G. BARNES[1] AND THOMAS D. NUDDS[1]

ABSTRACT.—Interspecific competition may shape species' niches such that relative niche positions remain consistent in niche space. However, during times when competition is relaxed, it has been hypothesized that significant rearrangement of species' niches occurs, both relative to each other and to available niche space. We compared microhabitat niche relationships among coexisting Horned Grebes (*Podiceps auritus*), Pied-billed Grebes (*Podilymbus podiceps*), and American Coots (*Fulica americana*) in aspen parkland near Minnedosa, Manitoba, from 1982 to 1984. Despite annual variation in the structure and abundance of microhabitats due to fluctuating water levels, niche relationships among grebes and coots remained relatively consistent. Coots generally occupied shallow sites with tall vegetation, and Horned Grebes used deep sites with little vegetation; both species used sites with little spatial complexity. Pied-billed Grebes occupied sites intermediate to those of the other species with respect to water depth and vegetation height, and used more spatially heterogeneous sites. In two low water years, overall niche separation was greatest along a depth-vegetation height dimension. In a high water year, niche separation was greatest along a spatial complexity dimension. Nevertheless, relative amounts of niche separation remained consistent; coots and Horned Grebes were always most different, and coots and Pied-billed Grebes were always most similar, in microhabitat use. These data support the idea that niche organization in this guild results from interspecific interactions rather than random processes. *Received 23 Jan. 1989, accepted 20 May 1989.*

Until the mid-1970s, interspecific competition was thought to be responsible principally for observed niche sizes, niche overlap, and relative abundances of species in ecological communities (e.g., Cody and Diamond 1975). Wiens (1977), however, thought that fluctuations in resource abundance, especially for vertebrates, should cause interspecific competition to be only periodically important as a factor influencing community structure. His "variable environments" hypothesis contended that populations of coexisting species in variable environments might compete only rarely during ecological "crunches."

The next decade witnessed vigorous debate about the importance of competition and the adequacy of the evidence for it (e.g., Strong et al. 1984). By the mid-1980s, the debate moderated (e.g., Diamond and Case 1986) coincident with the emergence of a "paradigm of scale" (Allen and Starr 1982). Accordingly, the variable environments hypothesis was recast as a specific example of the way that scale affects patterns in data and interpretations about the factors producing the patterns (e.g., Wiens 1986).

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For example, "snapshot" assessments of niche sizes, shapes and positions, and other attributes of communities of songbirds can produce very different results from one year to the next in variable shrubsteppe habitats (Wiens 1981; Wiens and Rotenberry 1979, 1980) and deciduous forests (Holmes et al. 1986). Wiens (1981) argued that this type of evidence was inconsistent with the classical view that competition both shapes species' niches and causes species to maintain relatively static positions in niche space.

Nudds (1982) described interspecific niche relationships among Horned Grebes (*Podiceps auritus*), Pied-billed Grebes (*Podilymbus podiceps*), and American Coots (*Fulica americana*) coexisting on small wetlands in a single year. Here, we report on subsequent years of observations of microhabitat niche relationships among the same species at the same site over a period when resource abundance fluctuated. We tested whether interspecific niche relationships varied among years or whether species maintained static positions in niche space relative to each other and to available niche space.

STUDY AREA AND METHODS

Data were collected from mid-April to early July, 1982 to 1984, on a 1.62 km^2 study area in aspen parkland approximately 10 km NE of Minnedosa, Manitoba (50°N, 99°W). The region periodically experiences drought; both water levels within wetlands and the number of wetland basins containing water vary from year to year. Six of the nine potholes on the study area were present in all three years and were used for this study. They included temporary (Type 1; Smith 1971), semipermanent (Type 3), and permanent (Type 5) wetlands. Complete descriptions of the area can be found in Nudds (1982).

The perimeters of each pothole were marked at 10-m intervals with wooden stakes and several microhabitat characteristics were measured at each grid point (see Nudds 1982). Water depth was measured to the nearest 1.0 cm in late April and mid-May of each year. Average depth for a quadrat was obtained from measurements at the four grid points which delineated it. Structural aspects of the emergent vegetation were measured using a profile board (see Nudds 1977) at each grid point. Vegetation density in each of four strata (0.25, 0.5, 1.0, 1.5 m above the water surface) was estimated as percent of the profile board occluded by vegetation. Proportions (p) of the total amount of vegetation were summed over the four strata (i), and substituted into $1/\Sigma p_i^2$, which is an index of the complexity of vertical microhabitat structure. Vegetation height was measured to the nearest 1.0 cm with a stick fastened to the profile board. The value of each variable for a quadrat was then calculated as the mean of the values for the four grid points delineating it. Also, the number of "islands" of emergent vegetation in each of three size categories (<0.3 m, >0.3 m but <1 m, and >1 m diameter) in each quadrat were counted. Island-size diversity was calculated from $1/\Sigma p_i^2$, where p is the porportion of all "islands" in the ith size category. In total, 20 structural attributes were used to describe microhabitats (see Table 1).

For purposes of comparing changes in water levels among years, mean maximum water depth for each pothole was obtained by averaging the depths of the four deepest quadrats.

Microhabitat use by *F. americana*, *P. auritus* and *P. podiceps* was observed from blinds entered before sunrise from mid-April to early July each year. Observations were made on

TABLE 1

FACTOR LOADINGS AND AMOUNT OF VARIANCE ACCOUNTED FOR BY PCA ON MICROHABITAT VARIABLES DURING 1982–1984

Variable	Description of variables	1982		1983		1984	
		PC1	PC2	PC1	PC2	PC1	PC2
Depth	Water depth	−0.70	−0.15	−0.39	−0.56	−0.86	0.17
L1	Vegetation density in each of 4 layers	0.90	−0.31	0.96	−0.10	0.92	0.16
L2		0.77	−0.37	0.88	−0.29	0.79	0.58
L3		0.27	0.03	0.40	−0.16	0.41	0.76
L4		0.13	−0.01	0.29	−0.11	0.27	0.57
SumL	Total vegetation density	0.66	−0.38	0.97	−0.17	0.87	0.45
P1	Proportion of vegetation at each layer	0.82	−0.18	0.92	−0.01	0.87	−0.24
P2		0.23	−0.29	0.39	−0.38	0.35	0.68
P3		−0.69	0.25	−0.95	0.12	−0.77	0.28
P4		−0.84	0.31	−0.96	0.13	−0.93	−0.20
Vegdiv	Vertical complexity of vegetation	−0.69	0.35	−0.92	0.12	−0.58	0.10
Height	Vegetation height	0.87	−0.21	0.90	0.05	0.75	0.23
N1	Number of "islands" in each of 3 size categories	0.42	0.64	0.23	0.74	0.65	−0.46
N2		0.67	0.53	0.14	0.77	0.74	−0.34
N3		0.56	0.06	0.50	0.32	0.70	−0.10
SumN	Number of "islands"	0.76	0.55	0.33	0.81	0.77	−0.42
NP1	Proportion of "islands" in each size category	0.46	0.64	0.09	0.67	0.69	−0.34
NP2	"Island size" diversity	0.54	0.35	−0.07	0.52	0.60	−0.20
NP3		0.35	−0.26	0.48	−0.30	0.39	0.06
Isldiv	Percent of variance explained	0.75	0.44	0.39	0.73	0.85	−0.18
λ_i		49.7	16.8	41.6	19.6	51.1	14.5

61, 74, and 59 days in 1982, 1983, and 1984, respectively, using spotting scopes and binoculars. The locations of individual coots and grebes were recorded on scale maps of each pothole at 0.5-h intervals for 4 h. Values for microhabitat characteristics for the quadrat in which an individual was recorded were assigned to that individual.

Stepwise discriminant function analysis (DFA, Nie et al. 1983), preceded by principal components analysis (PCA, Nie et al. 1983), was used to delineate species' differences in microhabitat use and to assign relative importance to those structural habitat features that segregated species. Species' scores on the PCs were used as orthogonal discriminating variables in DFA (Green 1979). Between-year variation in structural characteristics of microhabitat dimensions was quantified by comparing the variable loadings on the same PCs produced from separate analyses of data from different years (Rotenberry and Wiens 1980: 1242–1243, Landres and MacMahon 1983:186, Mulhern et al. 1985:475–476) using Kendall's ranked order correlations (Sokal and Rohlf 1969). If the ranked-order correlations were significant, we deemed the structure of the axes sufficiently similar for purposes of interannual comparisons of species' distributions along them. If they were uncorrelated, then inspection of the variable loadings would reveal how components of wetland structure varied interannually relative to one another. Finally, we examined between-year variation in species' pairwise niche separation (that is, the pairwise *F*-statistics, or among-to-within species variances in discriminant space [Nie et al. 1983]) and between year variation in mean niche position to see whether fluctuations in water levels across years affected niche relationships among grebes and coots.

RESULTS AND DISCUSSION

The numbers of observations of coots, Horned Grebes, and Pied-billed Grebes, respectively, in each year were: 1982: 205, 160, and 25: 1983: 624, 154, and 67; and 1984: 641, 59, and 124. Two microhabitat dimensions were identified by PCA each year and together accounted for 67%, 62%, and 66% of the total variance among the original microhabitat variables in 1982, 1983, and 1984, respectively (Table 1). In five of six between-year comparisons, the factor loadings for the microhabitat variables on the first and second principal components were significantly correlated (Table 2). In each year, PC1 described a continuum of microhabitat structure ranging from tall dense, spatially uniform stands of emergent vegetation in shallow water to deep, open water sites with no emergent vegetation (Table 1). Similar patterns of microhabitat structure were also evident in 1978 (Nudds 1982).

Correlations involving loadings from 1983, however, were lower than the correlation between loadings in 1982 and 1984 (Table 2). Increased water levels substantially altered habitat structure in 1983 (Fig. 1). Potholes in 1983 were characterized by a shallow, flooded perimeter of open water around stands of emergent vegetation which, in turn, surrounded deep, but also open, water in the centers of wetlands (Fig. 1). Thus, vegetation that was tall, dense, and in shallow water in 1982 and 1984 occurred at intermediate water depths in 1983, so the variable loadings

TABLE 2

KENDALL'S RANK CORRELATION COEFFICIENTS[a] BETWEEN VARIABLE LOADINGS ON PRINCIPAL COMPONENTS DESCRIBING MICROHABITATS USED BY GREBES AND COOTS IN 1982–1984

Component scores correlated	Principal component 1	Principal component 2
1982 vs 1983	0.58	0.66
1983 vs 1984	0.64	−0.62
1982 vs 1984	0.85	−0.43, NS

[a] Significant at the 5% confidence level ($P < 0.037$) adjusted for effects of non-independence among the 3 pairwise correlations for each principal component.

on PC1 in 1983 were not as tightly correlated with those of either 1982 or 1984 (Table 2).

Variables loaded differently onto PC2 in 1984 compared with 1982 and 1983. In all years, PC2 described a gradient in microhabitat complexity from uniform stands of emergent vegetation to more structurally complex stands highly interspersed by water (Table 1). In 1984, however, 16 of 20 variable loadings on PC2 changed sign compared with the same loadings in 1982 and 1983 (Table 1), and rank correlations between factor loadings in 1984 compared with 1982 and 1983 were negative (Table 2). We interpret this to mean that in 1984, PC2, relative to PC1, was rotated roughly in a direction opposite to that in 1982 and 1983. Thus, despite yearly differences in water levels that produced small differences in habitat structure described by PC1, PC2 described the same aspects of habitat structure in each year.

In all years, DFA identified both principal dimensions as important ecological segregators of species, although the relative importance of each dimension was not consistent among years (Table 3). In 1982 and 1984, overall microhabitat separation among species was greatest along the depth dimension (Table 3). Though microhabitat niche separation remained markedly high, it decreased after PC2 entered the discriminant model in both years (Table 3), reflecting the greater degree of species' separation along the depth gradient than along the spatial complexity dimension. In both years, species' pairwise niche separation was greatest between *F. americana* and *P. auritus* and less between *F. americana* and *P. podiceps,* and *P. podiceps* and *P. auritus* (Fig. 2).

In 1982 and 1984, shallow sites with tall vegetation were used by *F. americana, P. auritus* used deep sites with short vegetation, and *P. podiceps* was found at intermediate water depths and occurred in more patchy microhabitats than the other species (Fig. 2).

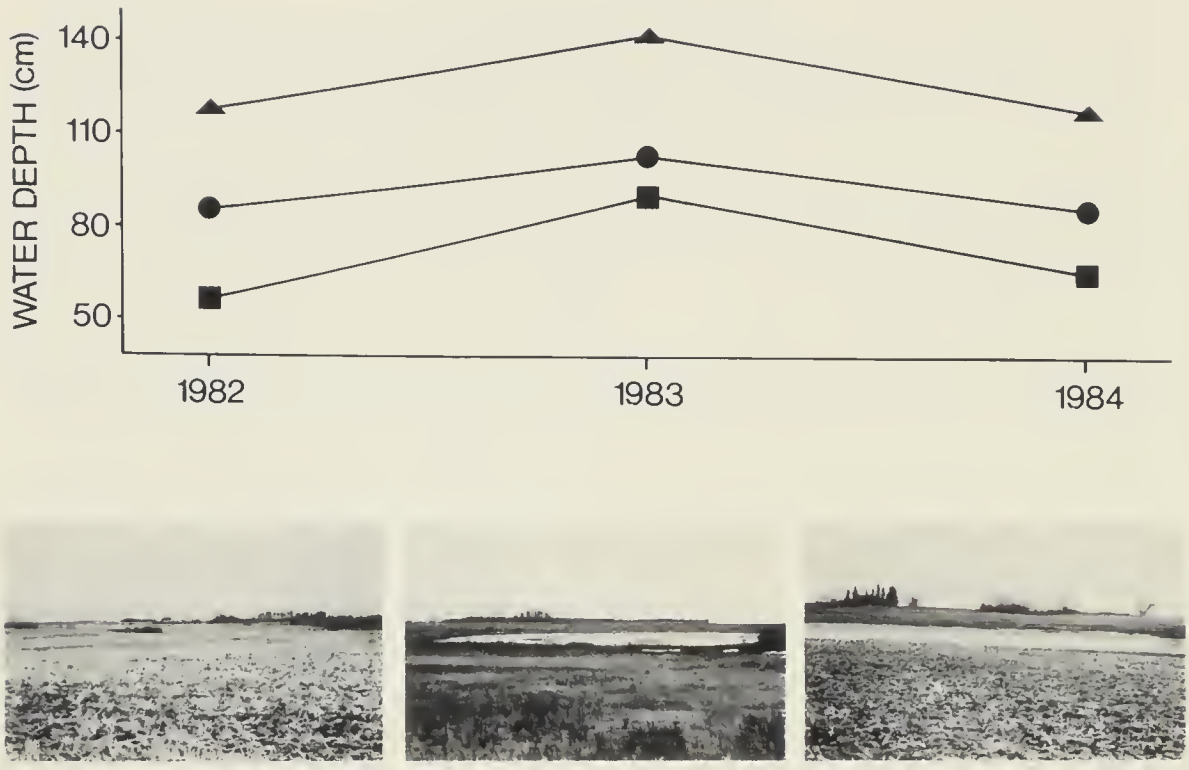

FIG. 1. (Upper) Mean maximum water depths of deep (▲), intermediate (●), and shallow (■) potholes used by grebes and coots from 1982–1984. (Lower) An illustration of wetland conditions from (left to right) 1982–1984 in a typical pothole. Note the flooded perimeter and ring of emergent vegetation in the wetland in 1983 (middle) compared with the other years.

In 1983, unlike 1982 and 1984, species segregated most along the spatial complexity dimension (Table 3). Again, the inclusion of the other microhabitat dimension (in this case, the depth gradient PC1) caused overall species' separation to decrease, although species still differed markedly in microhabitat use (Table 3). Also unlike 1982 and 1984, *F. americana* and *P. auritus* used sites very similar in vegetation height (PC1); but like 1982 and 1984, *P. podiceps* used patchier microhabitats than the other species. Like 1982 and 1984, niche separation was greatest for *F. americana-P. auritus* and less for the others (Fig. 2).

Nudds (1982) concluded that it was not necessary to invoke interference competition as an explanation for observed differences in microhabitat use among grebes and coots (Faaborg 1976). However, he could not resolve whether any other form of competition was responsible for the observed differences among species, because his was a "snap-shot" of differences in microhabitat use among species during a single season. Our study, however, identified patterns of microhabitat niche separation and position over three years that were similar to each other and similar to

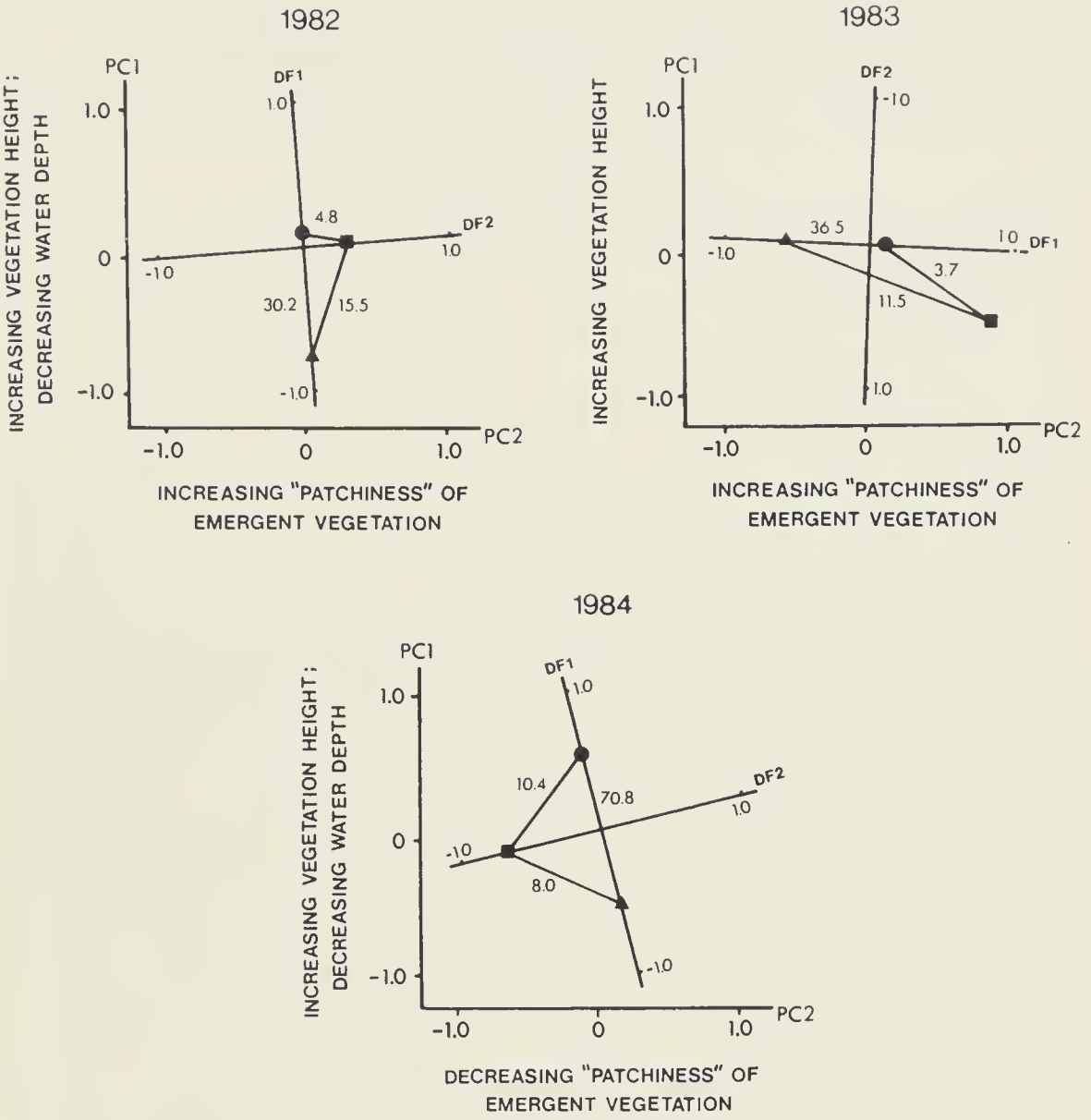

FIG. 2. Temporal variation in the microhabitat relationships among Horned Grebes (▲), Pied-billed Grebes (■), and American Coots (●) in two-dimensional space, and the discriminant axes along which species segregated. Numbers adjacent to lines connecting species' centroids are maximum ratios of among-to-within species variances in microhabitat use from discriminant analysis.

those found earlier (Nudds 1982). Thus, patterns of microhabitat use appear relatively robust to fluctuations in microhabitat abundance and distribution. The positions of species' niches, both relative to each other and relative to available niche space, were altered little despite that variation. This finding is consistent with the idea that microhabitat use by these species is determined more by biological interactions than it is by random assembly.

TABLE 3

OVERALL MICROHABITAT SEPARATION[a] IN DISCRIMINANT SPACE AFTER ENTERING THE FIRST AND SECOND PRINCIPAL COMPONENTS FOR THE GREBE-COOT GUILD AT MINNEDOSA, MANITOBA DURING 1982–1984

Year	Principal component[b]	*F*-value	*P*-value
1982	1	30.16	0.0001
	2	4.75	0.009
1983	2	43.84	0.0001
	1	30.19	0.0001
1984	1	70.54	0.0001
	2	35.75	0.0001

[a] Among-to-within species variance in discriminant space.
[b] Order selected for entry into the discriminant analysis.

Environments vary with varying amplitudes and periodicities. Further, attributes of communities of species with differing life-history traits might be expected to differ in response to variations in environmental conditions, that is, to differ in "tracking ability" (Roughgarden 1979:398, Boyce and Daley 1980). Wiens (1977) suggested that competition should be a temporally sporadic, often ineffective, interaction in variable environments and found little evidence that communities of shrubsteppe birds track fluctuating resources (Wiens 1986). Conversely, Cody (1981) thought that communities might track resource fluctuations and remain in a dynamic but resource-limited state. Nudds (1983), for example, thought that competition played a role in structuring waterfowl communities in variable environments. He suggested that over the long term, ducks tended to equilibrate population sizes with available resource levels because high fecundities and long life spans enable ducks to track fluctuations in resource abundance. Our results suggest that grebes and coots might respond to environmental variability more like ducks than shrubsteppe birds. Although grebes and coots live in variable environments, they nevertheless show relatively consistent niche relationships from year to year. Perhaps Wiens' (1977) "variable-environments" hypothesis is less appropriate for waterfowl, such as grebes and coots, if they can better track resource fluctuations than can short-lived shrubsteppe birds.

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ECOLOGY, BEHAVIOR, AND CONSERVATION OF THE POO-ULI (*MELAMPROSOPS PHAEOSOMA*)

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ABSTRACT.—Studies of the population density, habitat structure, foraging behavior, and activity budgets of the Poo-uli (*Melamprosops phaeosoma*) were conducted intermittently between 1973 and 1985 in a 50-ha study area in the upper Hanawi watershed, island of Maui, Hawaii. Poo-uli have apparently declined in density on this site by 80% from 1975 to 1981 and by 90% from 1975 to 1985. During this period, pig activity, as indexed by ground cover disturbance, increased 473%. Compared to values in the range of the Poo-uli, pig activity was 9–24 times greater in two adjacent out-of-range areas. Poo-uli most frequently foraged from 4–7 m height on ohia (*Metrosideros polymorpha*), olapa (*Cheirodendron trigynum*), ohelo (*Vaccinium calycinum*), and kanawao (*Broussaisia arguta*) in decreasing frequency; feeding on kanawao was significantly more frequent than random expectation. Chief food items were land snails and insects. Most prey were captured on branches from under moss, lichen, and bark by gleaning, probing, and pecking. Birds spent 48% of their daylight hours foraging and 30% quietly perching. Poo-uli frequently formed small mixed-species flocks, usually with Maui Creepers (*Paroreomyza montana*), that probably facilitated predator avoidance and foraging efficiency. The major limiting factors at present appear to be habitat modification from feral pigs (*Sus scrofa*), predation, avian disease, interspecific competition from the introduced garlic snail (*Oxychilus alliarius*), and possibly gene pool impoverishment. Control of pigs is recommended. *Received 9 Oct. 1986, accepted 20 May 1989.*

The Poo-uli (*Melamprosops phaeosoma*) is a drab, black-faced, short-tailed Hawaiian honeycreeper (Drepanidinae) that was discovered in 1973 on Maui, Hawaii (Casey and Jacobi 1974). It has proved difficult to find and elusive to study. Stomach analyses of two specimens suggest that the Poo-uli is one of the few passerines to feed extensively on molluscs (Baldwin and Casey 1983). Due to limited anatomical material and few life history reports, systematic relationships are uncertain, with the monotypic genus *Melamprosops* generally considered *incertae sedis* among the honeycreepers (Pratt 1979, AOU 1983). Because of this species' poorly known natural history, we report here on its abundance, range, habitat relation-

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ships, foraging behavior, social behavior, and factors that may limit its abundance and range.

STUDY AREA AND METHODS

Intensive studies on bird density, habitat structure, foraging behavior, and activity budgets were conducted in 1973–75, 1980–81, and 1984–85 on the Hanawi study area, a steeply sloping 50-ha site located at 1800–2100-m elevation between the branches of Hanawi Stream on the island of Maui, Hawaii (Fig. 1). The area supports a rainforest averaging 13 m in height and 60% crown cover, dominated by ohia (*Metrosideros polymorpha*) and olapa (*Cheirodendron trigynum*). The understory is composed of native subcanopy trees, shrubs, and ferns.

We laid a transect in the study area perpendicular to the contour from 1800- to 2100-m elevation with stations at 30.5 m elevational increments. At these stations we estimated the cover of all major plant species in 5 height strata delimited at 0.3, 1.5, 4.6, and 9.1 m and the percent of ground cover showing recent disturbance by the rooting and wallowing activities of feral pigs (*Sus scrofa*). In addition, we recorded foliage cover in 1 m height increments at 28 stations randomly located within the study area. Expected height use was computed from the foliage height profiles at the 28 random sample points using a goodness-of-fit analysis. The 0–1 m height interval was excluded from this analysis because the very dense vegetation in that interval obscured bird behavior and therefore probably biased observations.

Population densities were estimated in the study area using the variable circular-plot method (Reynolds et al. 1980). Estimates were based upon eight-minute counts and a Bayesian estimator (Johnson 1981) for the variance. Bird counts were made in 1975 at the 30.5 m elevational stations, in 1981 at the 28 random points, and in 1985 at 15 systematically placed points that were censused 2–4 times. We used an effective detection distance of 28 m for this species (Scott et al. 1986).

Data recorded on foraging behavior for each food item we observed or believed to be captured included: elevation, height above ground, plant species item was taken from, substrate (leaf, twig, branch), maneuver (peck, probe, glean, hover), and food item identity when determinable. To determine expected plant species use, we computed the relative abundance of each plant from the relative cover in the five height strata sampled at 30.5 m elevational increments; these covers were weighted by the amount of time birds were observed in each stratum at each elevational band. For sample size in statistical tests, we used the number of independent behavioral sequences observed (i.e., substantial difference in place or time between observations).

Activity budget data were gathered on birds observed during June 1974–August 1975 and May 1980–January 1985. For each observation of a focal bird, we recorded the elevation, height above ground, plant species of perch, activity type (sedentary activities: stationary perching, vocalizing, preening, defecating; locomotive activities: hopping, climbing, hanging, flying; foraging activities: active peering, gleaning, probing, pecking), duration of the activity, and associated bird species for as long as the bird was in sight. To reflect the relative amount of energy required for different activities, we estimated the metabolic cost of each activity as a multiple of the standard metabolic rate, using the values in Holmes et al. (1979) as guides. The standard metabolic rate multiples used for each activity were: perching 1.5, vocalizing 2, preening 2, defecating 2, hopping 5, climbing 5, hanging 5, flying 10, peering 2, gleaning 2, probing 2, and pecking 2. These values were multiplied by the amount of time birds devoted to each activity, the resulting values totaled, and percentages calculated to show the relative amount of energy expended in each activity.

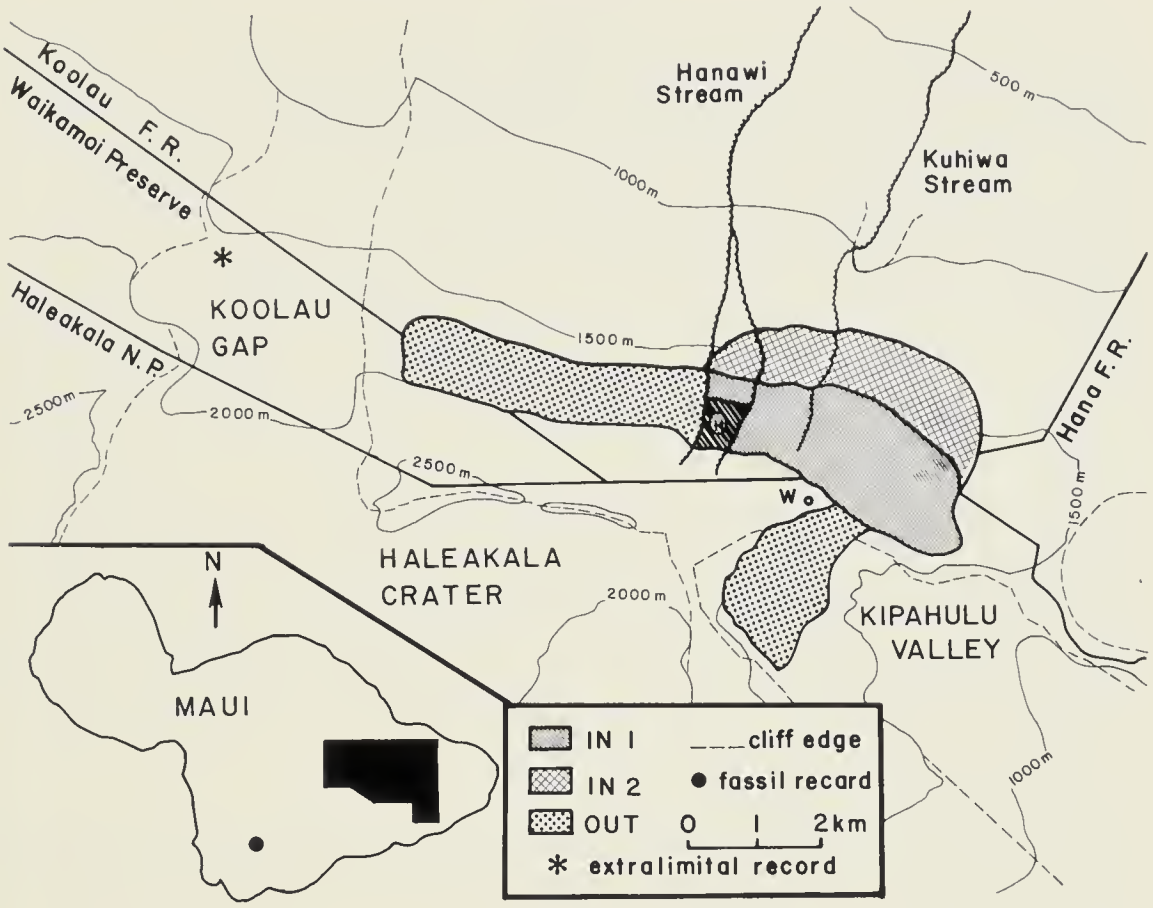

FIG. 1. Geographical distribution of the Poo-uli. H = Hanawi study area; IN-1 = area within range used in analysis of habitat features; IN-2 = remaining area within range not used in analysis; OUT = areas outside range used in analysis; W = Lake Wai Anapanapa.

Habitat features within the present range of the Poo-uli were compared with features in two adjacent areas outside the range, one west of the range, lying in the Koolau Forest Reserve between Hanawi watershed and Koolau Gap ("West Koolau"), and the other south in Kipahulu Valley (Fig. 1). These areas contained the same general habitat type, partly closed ohia forest. The lower elevational limit was 1675 m; the upper was determined by the upper limit of forest cover and varied from 2000 to 2100 m. The area within the range comprised the known range above 1675 m elevation. This elevation was chosen because these areas were well above the lower elevational limits of the Poo-uli, where range delineation was difficult, and above the upper elevational distribution of mosquitoes, to avoid the potentially confounding factor of avian disease (van Riper et al. 1986). Areas north or east of the range were not compared with the area within range because we suspect avian diseases borne by mosquitoes limit the distribution in those directions, based on the absence of other presumed disease-sensitive species (e.g., Maui Creeper). Data for comparing habitat features were collected in 1980 during the Hawaii Forest Bird Survey (HFBS). The HFBS used stations 134 m apart on parallel transects 1.6–3.2 km apart that were aligned perpendicularly to elevational contours (see Scott et al. 1986 for further details). At each station, canopy height, pig activity, and the areal cover of tree crowns, shrubs, herbs, and ground ferns were optically estimated by trained botanists following the methods described in Scott et al. (1986).

ECOLOGY

Range and habitat.—The Poo-uli is confined to an area of about 13 km^2 on the outer northeast slopes of Haleakala Volcano on the island of Maui in Hawaii (Scott et al. 1986). Given the extreme rarity and inconspicuousness of the species and the sampling intensity of the HFBS (15 counts/km^2), the range defined by Scott et al. (1986) may be conservative. Our records show that the range (Fig. 1) is bounded on the west by the west branch of Hanawi Stream, where understory modification by feral pigs increases substantially (HFBS data). Numerous scattered sightings east of the Hanawi study area indicate that the range continues eastward across the upper Kuhiwa watershed, ending somewhere in an unexplored region northeast of Lake Wai Anapanapa. The range of all sightings is 1400–2100 m elevation, with 80% of the sightings at 1800–2050 m. All sightings have been in ohia rainforest; most birds were seen in areas of relatively dense, moss-draped understories, frequently along gulches and other areas less disturbed by pig activity. The HFBS made three Poo-uli sightings, located over a 7.1 km distance along transect 9 in upper Kuhiwa and Hanawi watersheds, in a habitat mosaic of relatively pristine areas and others heavily impacted by pigs.

Poo-uli have not been reported from Kipahulu Valley, a comparatively well-studied area. One record made on The Nature Conservancy's Waikamoi Preserve in April 1983 (G. L. Holroyd, Canadian Wildlife Service, pers. comm.) lies 7.8 km west of the next nearest record and may represent a scattered low density relict population in and west of Koolau Gap. Several subfossils found at 500 m elevation on the dry leeward side of East Maui near Ulupalakua (H. F. James pers. comm.) suggest that mature dry mesophytic forests were also originally occupied and may have been the optimal habitat. This habitat has been almost totally altered to scrub vegetation and introduced plant communities through human and introduced ungulate activity.

Comparison of areas within and outside the range.—We compared an area within the present range of the Poo-uli to adjacent areas lying to the west and south, West Koolau and Kipahulu Valleys (Fig. 1). All three areas were above 1675 m elevation, had the same general habitat type, partly closed ohia-olapa forest, and harbored relatively high populations of Maui Creepers and endangered passerines (Scott et al. 1986).

At the level of resolution we used to describe the vegetation, only minor differences appeared in vegetation structure among the sites (Table 1). Significant differences in herb and fern cover appeared between the area within range and the West Koolau area, but Poo-uli were rarely observed using these substrates, and no difference in these habitat components appeared between the area within range and Kipahulu Valley. The con-

TABLE 1

HABITAT COMPARISONS OF AREAS WITHIN AND OUTSIDE OF THE CURRENT RANGE OF THE POO-ULI[a]

Feature	Within range	Outside of range			
		Week Koolau		Kipahulu Valley	
			P^c		P^c
N (sample size)	20	22		22	
Canopy height (m)	12 ± 3[b]	13 ± 3	0.52	12 ± 3	0.88
Percent					
Crown cover	58 ± 18	52 ± 11	0.22	60 ± 15	0.75
Shrub cover	57 ± 27	52 ± 15	0.41	64 ± 24	0.44
Herb cover	10 ± 8	5 ± 5	0.006	10 ± 11	0.90
Fern cover	66 ± 7	59 ± 5	10^{-4}	65 ± 23	0.78
Pig digging	1 ± 2	24 ± 21	10^{-7}	9 ± 12	0.002

[a] Out-of-range areas lie adjacent to areas within range.
[b] x ± SD.
[c] Two-tailed probabilities from t-test comparing values for areas within and areas outside of the range.

sistent difference between areas within and outside the range was pig damage; the range of the Poo-uli on the whole was restricted to areas of low or apparently recent pig damage. Pig damage averaged 9–24 times greater in areas outside the range. The areas within and outside the range have similar coverages of the major understory species that Poo-uli forage upon (species list in Table 2; $P > 0.05$ based on HFBS data).

Population estimates.—Poo-uli densities in the Hanawi study area declined from 1975 to 1985. In 1975 we estimated a density of 76 ± 8 [SE] birds/km^2 (N = 22 bird counts); in 1981, 15 ± 7 birds/km^2 (N = 28); and in 1985, 8 ± 4 birds/km^2 (N = 45). Density values declined 80% from 1975 to 1981 ($t = 5.7$, $P < 0.0001$) and 90% from 1975 to 1985 ($t = 7.6$, $P < 0.0001$). Opportunistic observations by Casey during 1973–83 and by Kepler, Mountainspring, and Scott during 1980–86 corroborated the decline, suggesting that it was not merely random variation. Although the high density in 1975 may have been a population peak attributable to favorable environmental conditions in the preceding years, the low values to which the density fell by 1981 indicates cause for concern. The 1980 HFBS reported a mean value of 11 birds/km^2 across the range (Scott et al. 1986), indicating that the values in the Hanawi area were relatively typical in 1981 for other areas in range.

BEHAVIOR

Foraging behavior.—Heights of Poo-uli perching and foraging sites had a slightly skewed distribution (Fig. 2) averaging 4.9 ± 1.9 [SD] m, indi-

TABLE 2

PERCENT PLANT SPECIES USE BY THE POO-ULI COMPARED WITH VEGETATION COMPOSITION

Plant species	Frequency of use		χ^2
	Observed	Expected[a]	
Ohia (*Metrosideros polymorpha*)	43.9	38.5	0.6
Olapa (*Cheirodendron trigynum*)	18.3	11.5	3.3
Ohelo (*Vaccinium calycinum*)	11.0	15.4	1.0
Kanawao (*Broussaisia arguta*)	6.1	0.9	24.2[b]
Kolea (*Myrsine lessertiana*)	6.1	8.5	0.5
Kawau (*Ilex anomala*)	4.9	1.7	4.9[c]
Pilo (*Coprosma ochracea*)	3.7	8.2	2.0
Other plants[d]	6.1	15.3	4.5[c]
Total	100	100	41.2[b]

[a] Based on vegetation composition at the foraging sites.

[b] $P < 0.001$, goodness-of-fit test based on a sample size of 82 independent behavioral sequences weighted by the number of feeding observations in each sequence (N = 171 observations).

[c] $P < 0.05$.

[d] Akala (*Rubus hawaiiensis*), alani (*Pelea* spp.), pukiawe (*Styphelia tameiameiae*), and naenae (*Dubautia* spp.).

cating extensive use of the understory and subcanopy. Compared to the foliage height profile above 1 m (Fig. 2), foraging sites were more often selected at 4–7 m height than expected by chance $\chi^2 = 51.0$, df = 1, $P < 0.0001$). On three occasions, we noted birds foraging in the ground layer. Because of the concealing nature of the foraging column at heights below 1 m, we may have missed some birds foraging there.

Plants most frequently used as foraging sites were ohia, olapa, ohelo (*Vaccinium calycinum*), kolea (*Myrsine lessertiana*), and kanawao (*Broussaisia arguta*) (Table 2). Use of these plants was not random based on the relative foliage composition at the elevations and heights that the behavior was observed ($\chi^2 = 41.2$, df = 7, $P < 0.001$). For example, Poo-uli used kanawao, a 1–2 m high shrub, six times as often as expected based on availability. This was probably related to food levels, as kanawao foliage had higher densities of native snails than other understory species. Kanawao foliage comprised 12% of the total foliage volume in the 0.3–1.5 m height class, but 37% of the native snails found (N = 24) were on kanawao ($\chi^2 = 14.0$, df = 1, $P < 0.001$). Infrequent visits to pukiawe (*Styphelia tameiameiae*), akala (*Rubus hawaiiensis*), and ground ferns (mostly *Dryopteris wallichiana*) may reflect the relatively few snails we noted on these plants (33% of the total foliage volume v. 8% of the snails found; $\chi^2 = 6.8$, df = 1, $P < 0.01$).

Poo-uli fed primarily by gleaning, probing, and pecking prey items from branch and leaf substrates (Table 3). The most frequently used substrates

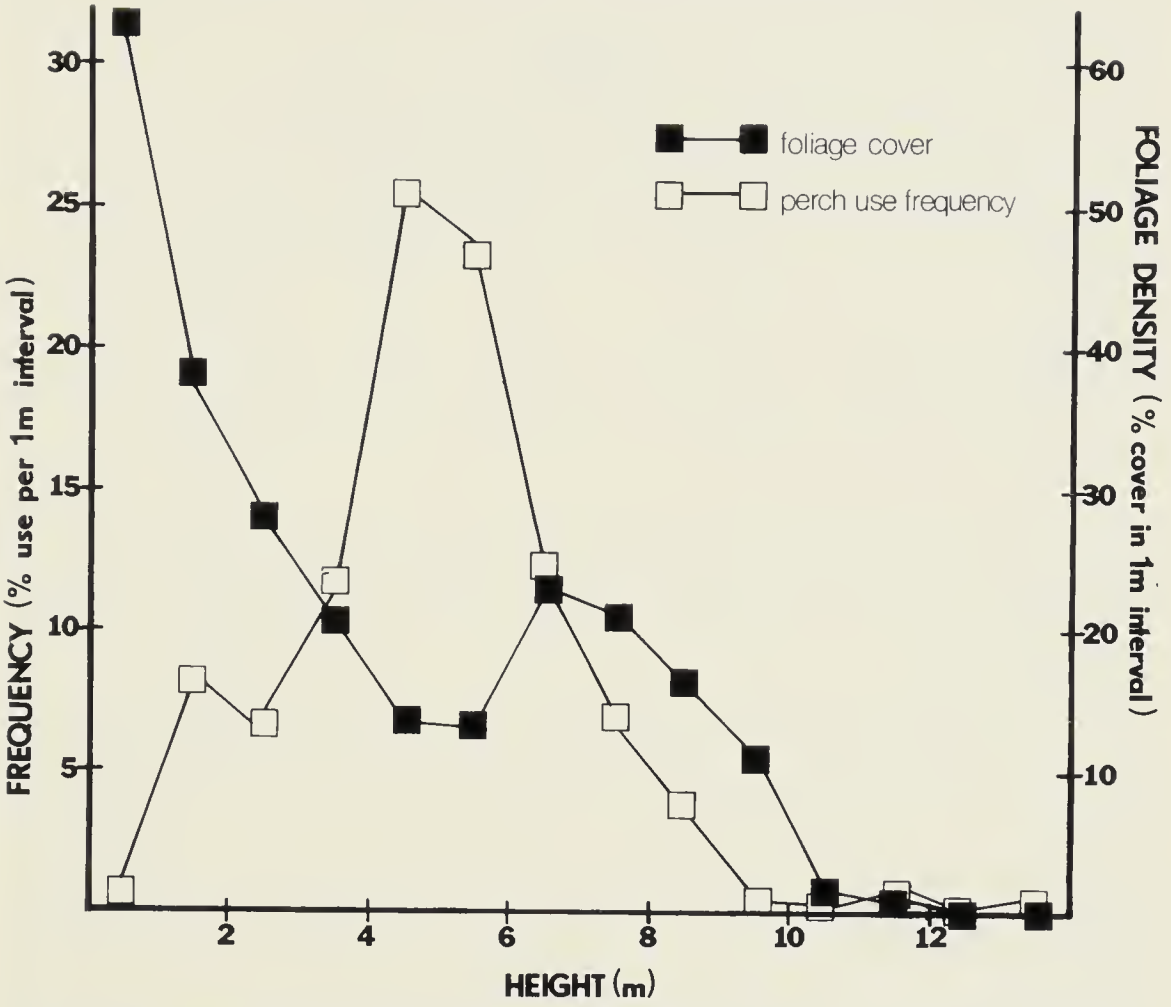

FIG. 2. Frequency of perching compared to foliage coverage in 1-m height intervals.

(85% of all prey captures observed) were branches where small invertebrates were captured by gleaning, prying into cracks, tearing up bits of lichen and moss, and more rarely by flaking off bits of bark. Birds often pulled up lichen and moss mats in search of prey.

Poo-uli were observed feeding on small tree snails (N = 7), insect larvae (6), insect adults and spiders (5), and olapa fruits (2). These observations corroborated an analysis of two stomachs (Baldwin and Casey 1983) that contained small snails (63% of 465 items), arthropod adults (28%), insect larvae (5%), and olapa fruits (4%). The lower proportion of insect larvae in the stomachs analyzed may represent sampling error or the faster digestive rate for soft-bodied prey. The presence of seven ground beetles (Carabidae) in each stomach indicates occasional ground foraging, which is also suggested by the bird's drab color and stout pedal morphology. Similar color patterns of brown and black occur among many antbirds (Formicariidae) that feed on the forest floor (Meyer de Schauensee and

TABLE 3
FORAGING BEHAVIOR OF THE POO-ULI BY SUBSTRATE AND MANEUVER

Substrate type	Maneuver type				Total
	Peck	Probe	Glean	Hover	
Leaf	0	11	9	1	21
Twig	0	3	1	0	4
Branch	20	42	84	0	146
Total prey captures	20	56	94	1	171

Phelps 1978). The snails and insects taken by Poo-uli were usually partly concealed among lichen, moss, and bark. Twice, Poo-uli were seen handling larger snails (>5 mm length) for 10–30 sec after capture to remove part of the shell.

The morphology of the Poo-uli appears to be adaptive for several aspects of its feeding behavior. The large, stout toes may be adapted for foraging for tree snails by prying up moss and bark. The stout bill may reflect the force needed to manipulate snails. Bock (1978) noted that the species has a distinctive spoon-shaped tongue with strong associated musculature; this would appear to be adaptive for prying prey from substrate refugia and for extracting larger snails from their shells.

Activity budget.—Poo-uli spent 48% of their day and 40% of their energy foraging (Table 4), although they were most frequently seen quietly perching, and less frequently peering or gleaning. Locomotive activities represented 15% of the diurnal time budget and about 36% of the energy budget. Our data on the activity budget of the Poo-uli are in conformance with that of typical passerine birds (King 1974).

Flocking behavior.—In 46% of 28 sightings, Poo-uli were in loose flocks with Maui Creepers; two of these flocks also included a Maui Parrotbill (*Pseudonestor xanthophrys*). Typically, one or two Poo-uli associated with two to five Maui Creepers. Interspecific aggression was noted once, when a Poo-uli chased a Maui Creeper that had approached to within 1.5 m. Flocking may be facilitated by Poo-uli and Maui Creeper chip notes, which are very similar to each other.

Several times, one or more birds in a mixed-species flock examined the foraging site where another bird had just captured prey, and then examined other similar sites in the vicinity. On several occasions Short-eared Owls (*Asio flammeus*) were observed quartering low over the forest canopy. At these times, the birds in the mixed flock gave alarm notes and retreated quietly into denser cover.

TABLE 4
DIURNAL ACTIVITY BUDGET OF THE POO-ULI

Activity	Percent of time[a]	Percent of energy
All sedentary activities	36.4	23.9
Stationary perching	29.5	18.2
Vocalizing	3.9	3.2
Preening	2.9	2.4
Defecating	0.1	0.1
All locomotive activities	15.3	36.4
Hopping	7.1	15.0
Climbing	3.7	7.6
Hanging	2.3	4.7
Flying	2.2	9.1
All foraging activities	48.2	39.7
Active peering	18.3	15.1
Gleaning	18.0	14.8
Probing	10.2	8.4
Pecking	1.7	1.4

[a] N = 5003 seconds.

The flocks we observed seemed typical of mixed flocks in continental areas, although our heuristic observations indicated that flock cohesion was lower and on the order of several minutes rather than hours. Flocking of Poo-uli with Maui Creepers was noted in Berger (1981) and Shallenberger (1981) and dispels the concept advanced by Willis (1972) that mixed-species flocks are absent in the Hawaiian avifauna. Mixed-species flocks are known from Fiji, which also has diurnal avian predators, but not from Samoa or Micronesia which lack such predators, suggesting predator avoidance as a selective force (H. D. Pratt, in litt.). Recent fossil finds in the Hawaiian Islands indicates that extinct hawks and owls morphologically adapted to catching small land birds may have been numerous prior to Polynesian contact (Olson and James 1982).

Vocalizations.—Poo-uli are relatively quiet, vocalizing about four percent of the day (Table 4). A developed song similar to that of other Hawaiian honeycreepers has never been observed. Most frequent vocalizations are single chip notes. Single chip notes are difficult to distinguish from those of the Maui Creeper. Also frequently given is a series of 3–4 chip notes, the first often emphatic and followed by a short pause (ca 0.5–1 sec), with the remaining notes given in quick succession at a slightly lower pitch and volume. This series has a characteristic "burry" quality and is a distinctive vocalization. Short *tschew* notes and a fast *chi-chi-chi*

series have been noted when immatures were in the area and may be alarm notes.

CONSERVATION

Limiting factors.—Several factors may presently limit the range and numbers of the Poo-uli: (1) habitat modification, (2) predation, (3) avian disease, (4) interspecific competition, and (5) gene pool impoverishment.

In the Hanawi study area and most montane rainforests in Hawaii, the principal agent of habitat modification is the feral pig. As documented for similar forests on the island of Hawaii (Giffin 1978, Baker 1979, Ralph and Maxwell 1984) and elsewhere (Tisdell 1982), rooting and wallowing activities of feral pigs cause extensive damage to native ecosystems by radically altering the understory composition, hindering forest regeneration, facilitating invasion of introduced pest plants (Mueller-Dombois 1981), and leading to severe soil erosion on steep slopes (USFWS data). In addition, pig activity generates mosquito breeding sites, which may assist mosquitoes in establishing populations at higher elevations (Scott et al. 1986, Van Riper et al. 1986). Although pigs were introduced by Polynesian colonists, substantial populations were not thought to have been established in montane forests until after European pigs were introduced (Tomich 1969, Warshauer 1980).

The analysis of areas within and outside the Poo-uli range (Table 1) suggests that pigs are a significant limiting factor. Quantitative surveys of pig activity in the Hanawi study area showed a significant increase from 1975 to 1983 (Fig. 3; $P < 0.002$, sign test). The percent ground cover disturbed by digging increased an average of 431% (range = 33–1500%). Present levels of pig activity now approximate values for adjacent areas lying outside the range (Table 1). Circumstantial evidence thus suggests that the decline in Poo-uli abundance on the Hanawi study area during 1975–85 was related to the rise in pig activity during this period.

Disruption of the ground cover by pig activity may reduce native snail populations, because many snail species graze extensively on terrestrial foliose lichens, and some species depend on the ground layer for their life cycle or during drought periods. Pig activity may promote dispersal of the introduced garlic snail (*Oxychilus alliarius*), which is predatory on other land snails, occurs in numbers on Maui at high elevations, and appears to be well adapted to disturbed habitats (Severns 1984).

The garlic snail is probably a very effective competitor for food resources with the Poo-uli. Severns (1984) has suggested that predation by the garlic snail has decimated populations of native land snails, particularly ground species. Garlic snails were probably introduced during World War II (Cooke and Baker 1947) and are abundant in montane rainforests on

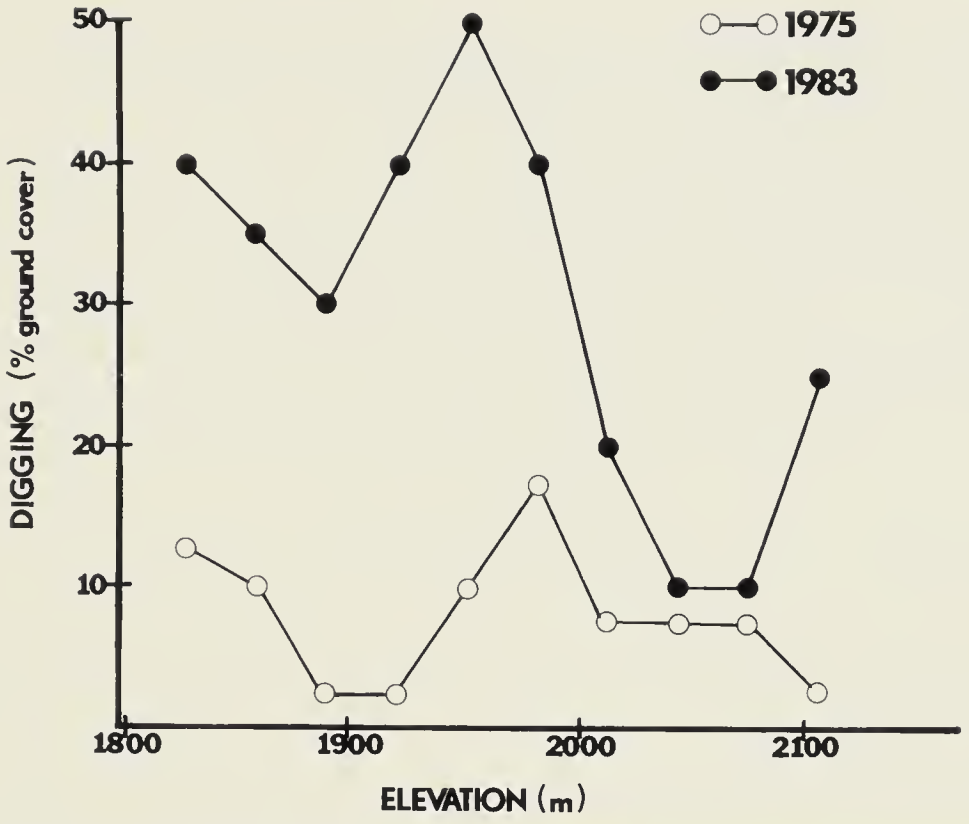

FIG. 3. Percent surface area disturbance by pig digging along an elevational transect in the Hanawi study area, 1975–83.

Maui. In two plots in the Hanawi study area, we found 133 ± 33 [SE] live snails/m^2 on localized mossy substrates, and nearby we saw thousands more empty shells of the same species. Garlic snails may substantially deplete the Poo-uli food base; their edibility to Poo-uli is unknown, and they are infrequent in the understory. Since their introduction, garlic snails may have had a major, hitherto unsuspected impact on the Poo-uli.

Interspecific competition for food resources from other birds is probably minor for the Poo-uli because of its distinctive foraging niche. Mountainspring and Scott (1985) found that competition between native and exotic birds in Hawaii was relatively minor for species whose foraging niches did not extensively overlap.

The low foraging height and frequent use of understory substrates may make Poo-uli vulnerable to mammalian predators. Substantial populations of the black rat (*Rattus rattus*) and the Polynesian rat (*R. exulans*) occur as high as 2000 m elevation in the study area, and unidentified feathers have been found in the stomachs of both species (R. T. Sugihara pers. comm.). Atkinson (1977) hypothesized that because of its arboreal habits, the black rat in particular had a significant negative impact on native birds (Perkins 1903). Cats (*Felis catus*) have been observed ten

times in the study area. The small Indian mongoose (*Herpestes auropunctatus*) may also be an occasional predator of Poo-uli because of its ground feeding habits (Baldwin et al. 1952).

The endemic Hawaiian avifauna evolved in the absence of many disease factors prevalent in continental areas. Many species show marked susceptibility to, and occasionally demonstrate mortality from, introduced mosquito-borne avian diseases, particularly avian malaria and pox (Warner 1968, van Riper and van Riper 1985, van Riper et al. 1986). On Maui, the lower elevational range limits for the Poo-uli, Maui Creeper, Iiwi (*Vestiaria coccinea*), and other endangered passerines lie near the upper limit for mosquito vectors. These lower elevational limits are probably at least, in part, determined by disease (Scott et al. 1986). Based on circumstantial evidence, Mountainspring (1986) estimated that 80% of the presently available suitable habitat is unoccupied by Poo-uli because of the presence of disease vectors.

The fossil records from areas that were formerly dry mesophytic forest suggest that the Poo-uli originally had a wider distribution and higher numbers before Polynesian contact (ca 400 A.D.). Scott et al. (1986) hypothesized that the present range comprises only about 1% of the original range. Quite possibly the present range is suboptimal or marginal habitat. The population, estimated at 140 birds in 1980 (Scott et al. 1986), has probably lost some genetic variability originally present, based on calculations of minimal population sizes needed to ensure long-term maintenance of rare alleles (Franklin 1980, Soulé 1980, Schonewald-Cox et al. 1983). Reduction in genetic variability could lead to reduced ability to adapt to novel environmental perturbations such as pig activity, introduced competitors, or climatic changes.

Management recommendations.—Because our data indicate that increased pig activity was highly correlated with the 1975–85 decline of the Poo-uli, and a likely contributor to its decline, the most pressing management action needed is reduction and control of pigs within the Poo-uli range. We recommend that pig-proof fences be constructed and pigs removed from the upper Hanawi and Kuhiwa watersheds (see Kepler et al. 1984). Control of pigs in montane rainforests should lower disease vector levels, improve watershed quality, and possibly reduce garlic snail populations as the ground cover regenerates.

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Wilson Bull., 102(1), 1990, pp. 123–130

SHORT COMMUNICATIONS

Display repertoire and social organization of the White-fronted and White-throated manakins.—The ecological, behavioral, and morphological variability observed among the 51 species of Pipridae (Snow 1979) is ideal for studying evolution of leks and the effects of sexual selection on speciation (Bradbury 1981, Prum and Johnson 1987). For example, several types of spacing patterns and male strategies have been described. The best studied manakin species form "classical leks" or "true leks" (Bradbury 1977, 1981; Oring 1982) in which males holding densely grouped individual territories perform competitive displays (i.e., White-bearded Manakin [*Manacus manacus*] [Snow 1962a; Lill 1974a, b] and Golden-headed Manakin [*Pipra erythrocephala*] [Snow 1962b, Lill 1976]). In "exploded leks" or "quasi-leks" (Gilliard 1963, Bradbury 1981, Oring 1982), individual males are more widely separated than in "classical leks"; they often display in auditory rather than in visual contact from sites that appear markedly clumped only when considering total home ranges (Bradbury 1981, Oring 1982, Bradbury and Gibson 1983, Foster 1983, Bradbury et al. 1986, Beehler and Foster 1988). In "classical" as in "exploded" leks, males may cooperate to attract females, although a single dominant male engages in pre-copulatory courtship display and copulation (review in Foster 1985).

During a study of seven sympatric species of Pipridae in French Guiana, I noted that courtship displays and social organization of the White-fronted Manakin (*P. serena,* nominate sub-species) and the White-throated Manakin (*Corapipo gutturalis*) differ from the previous descriptions given by Prum (1985, 1986). I present here my observations on the mating systems of these two species.

My study was made during two years of field work including three successive reproductive seasons (1985–1987): 18 months on the "Piste de St-Elie" site (5°04′N, 53°18′W, primary forest with secondary vegetation along the track, site described in Sabatier 1985) and five months in intact primary forest around a granite inselberg ("Inselberg des Nouragues," 4°05′N, 52°40′W, site described in Erard et al. 1989).

White-fronted Manakin.—Prum (1985) identified in Suriname "exploded" type leks in which the males, established in one well-determined area, perform both solitary and coordinated displays on their own or on another male's territory. Since no copulation was observed, it is impossible to define the precise role of such coordinated displays in this species breeding system. However, Prum (1985) observed female visits to males during both solitary and coordinated display, and he concluded that the coordinated displays appear to be more competitive than cooperative.

In French Guiana, I color banded 25 individuals (18 adult males) on three arenas and observed five arenas (formed, respectively, by eight, six, six, five, and five males) during 48 days (475 h). I also monitored by radio-tracking the activity of six individuals during 45 days (530 h).

My observations of displays of White-fronted Manakins are similar to those of Prum (1985), with the significant addition of the full behavioral sequence leading to copulation (Fig. 1). At the approach of a female, the male first flies between two horizontal perches producing a low rustling sound with his wings, and then performs a series of rapid flights between vertical perches on which he lands facing the center of the arena. The female joins him following his flights between perches. Male and female then restrict their display to two vertical perches between which they cross each other in flight. Prum (1985) describes the same display performed by a single male or a pair of coordinated males. During my study, 87 courtship displays were observed. Copulation occurred on only three occasions, during which the male flew above the female as they crossed between perches. It is possible

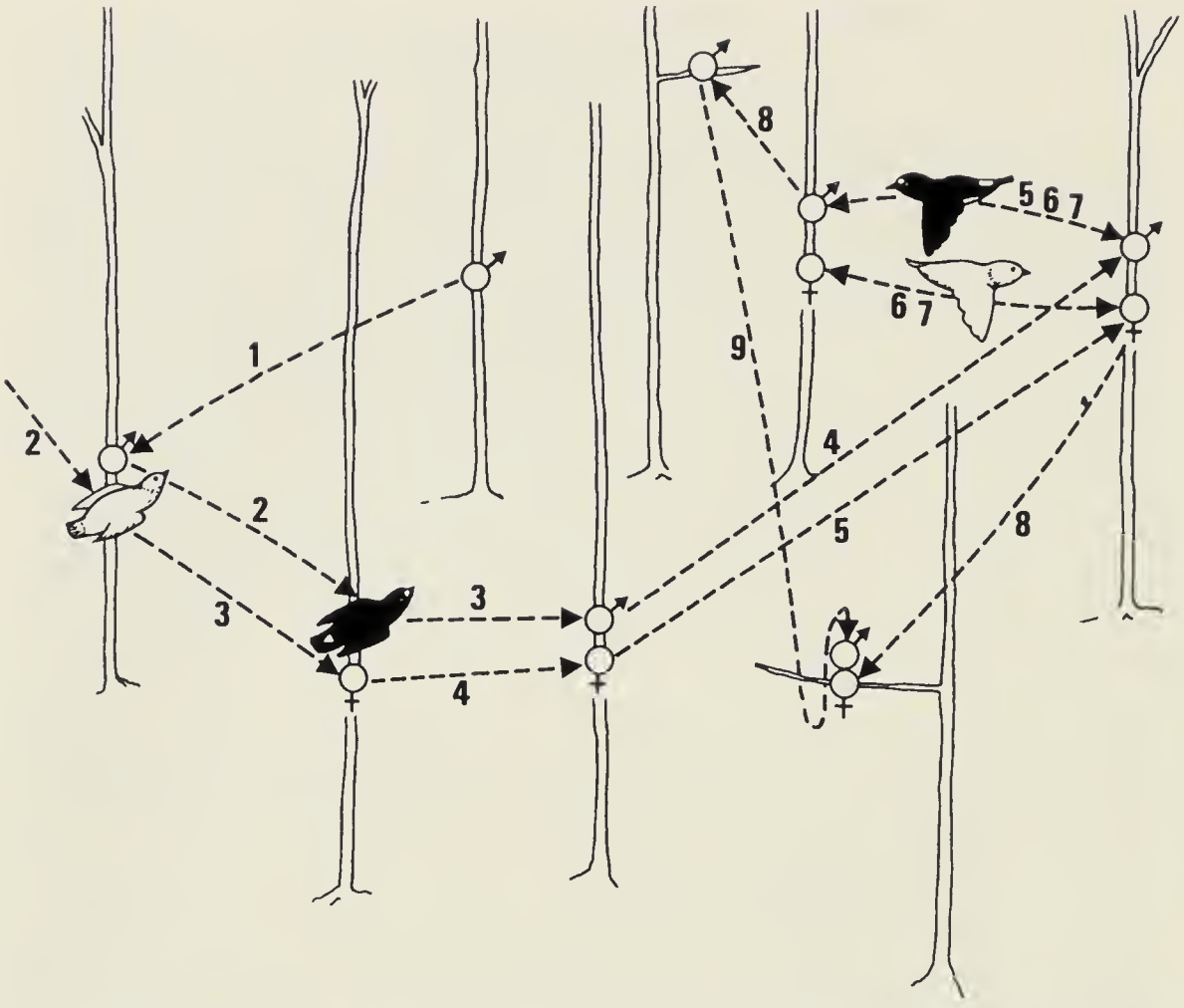

FIG. 1. Schematic representation of the *Pipra serena* courtship display: (1) Last of a series of flights by the male between vertical perches. (2 to 5) Simultaneous flights by male and female between 5 and 10 vertical perches. (6 and 7) The male and female cross each other several times in flight between perches, the male flying higher than the female. (8) The male perches above the female who has landed on the perch where copulation will take place. (9) S-shaped display flight: the male approaches the perch from below, then lands directly on the female for copulation.

that the female's lower position is a signal indicating that she accepts copulation, as in the White-bearded Manakin (Snow 1962a). The female then landed on a thin branch 1 or 2 m above the ground while the male settled on a perch above her. The male then performed a ritualized display flight tracing a horizontal S-pattern in the air (Prum 1985), approaching the nuptial perch from below, and landing directly on the female for copulation. The same display flight has been described in the Golden-headed Manakin (Snow 1962b, Sick 1967, Lill 1976). The entire behavioral sequence is very similar to the performance of the courtship display by Blue-crowned Manakins (*P. coronata*), although in *Pipra coronata* the coordinated "dance" display frequently was performed between males after the nesting season, females visited only single males.

In *Pipra serena,* coordinated displays between males are performed between an established territorial male and unrelated, non-resident males (Prum 1985). I observed in French Guiana 46 displays between males: 27 before the breeding season when adult males were establishing

their individual territories, 15 after the breeding period, but only four when the females were visiting the arenas. The males involved were mostly residents banded at the same arena during the previous breeding season (N = 42), unbanded adult males (N = 22), immature males in transitional plumage (N = 18) or adult males in their second year (N = 10). Coordinated displays frequently occurred in response to the invasion of display territories by non-resident males (46 displays for 67 invasions). On 31 occasions, the invading male followed the resident in his rapid flights among the low trees and shrubs of the understory. The territorial conflict stopped when the invading bird left the territory after the series of rapid flights (N = 21) or when he displayed like a female, flying lower than the resident male when they crossed between two perches (N = 23). On four occasions the visitor alighted momentarily on the nuptial perch of the resident male. These evidences support the conclusion of Prum (1985) that in *Pipra serena* the coordinated displays are more competitive than cooperative. Although Prum (1985) observed a female visiting a pair of displaying males, copulation in *Pipra serena* seems to occur only when females are visiting single males, as in *Pipra coronata.*

The spacing patterns of males measured during three successive reproductive seasons showed that White-fronted Manakins form "classical leks" in French Guiana. On each arena, five to eight males called and displayed in close proximity, each one occupying a 4–6 m diameter area within a 15–18 m diameter arena. The mean distance between the males and their nearest neighbor was 5.6 ± 1.2 m [SD] (N = 35). In addition, the lek of *P. serena* in French Guiana is not restricted to a single spot. Five groups of males systematically moved from an initial site, only used early in the day (visits of females from 6:30 to 9:30) to a second site, located 80–100 m lower down on the slope, only occupied later in the day (visits of females from 11:30 to 15:00). During the breeding season, all banded males (the 15 residents of three arenas observed during 21 days) and all radio-tracked males (three residents of different arenas followed during 24 days) showed a similar daily movement and used the same display territories. Each male defended both territories against the intrusions of unestablished males or neighbors and called throughout the day, with two periods of increasing activity when females visited the arenas. During 36 h each of three banded males was on territory 78%–86% of the day (72% to over 90% in Prum 1985). Among three copulations observed at three different arenas, two occured in the morning between 7:00 and 9:00 (at the "morning locality") and one at 13:00 (at the "midday locality"). This displacement of the group of males appears to be linked to the intensity of light available in particular forest areas at particular times of the day. The most illuminated areas were at the tops of thc slopes at dawn and farther downward in the valleys at midday. The males were moving every day from one spot to another during set display hours in order to benefit from better lighting conditions with respect to the very dark surrounding areas. Because of the regular use of two display sites by *P. serena* in French Guiana, I refer to this type of mating system as a "double-spot lek," in opposition to previously described leks which are restricted to a single spot. This terminology is independent of the dispersion patterns of males within the arena (i.e., classical or exploded leks).

These observations reveal the existence of geographic variation in *Pipra serena*'s lek behavior. Prum (1985) identified "exploded" leks in Suriname, and I found "classical" leks in French Guiana. In addition, Prum (1985) observed a male singing persistently from a single territory for over 70–90% of 5-min periods distributed throughout the day, whereas I described the existence of a "double-spot lek." This geographic variation could be related to different environmental conditions in the studied localities, among which eventual differences of illumination in the understory. For example, in Suriname males could display at a single site with good light exposure all day long, whereas in French Guiana they had to move from one locality with good light exposure in the morning to a site better illuminated

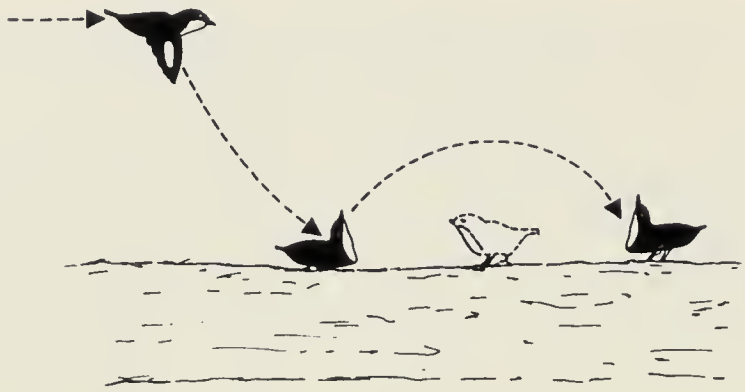

FIG. 2. Display flight of an adult *Corapipo gutturalis* above a subordinate male (dotted line). The bird points his raised throat toward the intruder, a posture he maintains for some seconds after having landed on the fallen log (cf. "performance of the display call," Prum 1986).

at midday. This evidence supports the "hotspot model" of lek evolution (Bradbury and Gibson 1983, Bradbury et al. 1986) because it suggests that males initiate the process of clumping and use two courtship locations in order to meet as many females as possible.

White-throated Manakin.—Prum (1986) described the existence in Suriname of "detached or mobile leks," based on limited observations of competitive displays by several adult and immature males together on a series of moss-covered logs. Davis (1949) observed copulation following competitive display by a group of six or more males and females. I studied six arenas in French Guiana for 57 days (610 h) distributed over three successive reproductive seasons. Five adult males, three females, and two immature males in transitional plumage were banded in a single lek. Observations were carried out when the males established their individual territories after an erratism period lasting from August to the end of September (dry season, 23 days of observation), and when females visited frequently the arenas during the breeding season (rainy season, 34 days of observation). My observations of the display repertoire of White-throated Manakins are very similar to those of Prum (1986), with the addition of the full behavioral sequence leading to copulation. However, I noted in French Guiana a context-dependent variation of fallen log displays. I observed 129 times the "performance of the display call" (Fig. 2) described by Prum (1986). This display was essentially performed between males in the absence of a female (85 times) and by solitary males (44 times), but never by a single male in the presence of a female. It was often observed when males were establishing their individual territories before the breeding period (67 displays by groups of males, 44 displays by solitary males) and more rarely during the breeding period in the absence of a female (18 times). In fact, during the "performance of the display call," the male seems to express dominance by passing over subordinate individuals and displaying his raised throat-patch toward the intruder. These observations are consistent with the descriptions given by Prum (1986): in Suriname the log-approach display, in which the male lands on the log and rebounds forward (over another individual if present) and facing back toward where he first landed (Fig. 2), was commonly performed between competitive males. In addition when Prum (1986) observed a female on a log, the male walked backward toward her immediately upon landing in a position which necessarily requires the male facing away from the other individual present and not facing toward him such as when he displayed competitively in front of an intruder.

During the complete courtship display cycle (Fig. 3), the ritualized display flight with synchronous calls ("display call," Prum 1986) and flashing of white wing-patches is followed

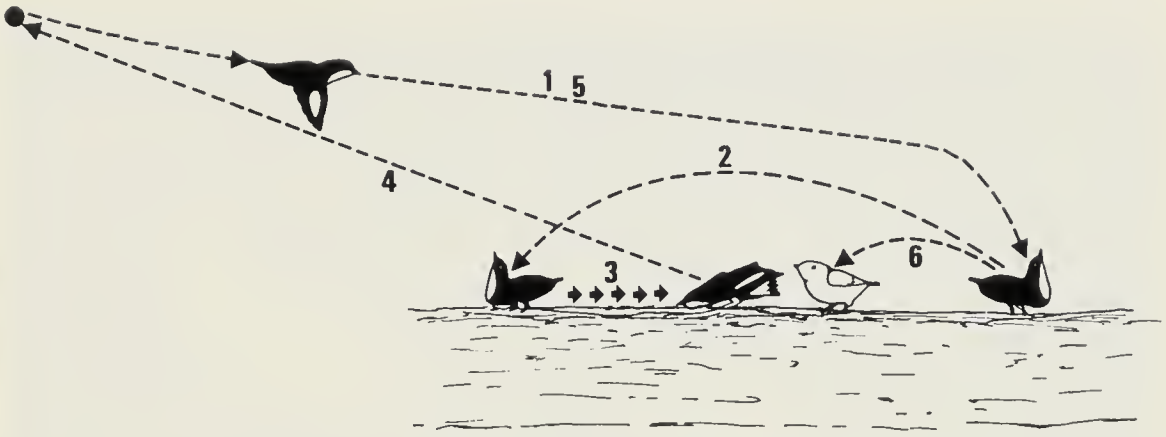

FIG. 3. *Corapipo gutturalis* courtship display in the presence of a female: (1) stereotyped display flight with synchronous calls. Landing with throat displayed to the outside, the male flaps his wings noisily, then rebounds directly backwards over the female. (2) Rebound in the direction from which he came, facing out the original direction of flight. (3) After having maintained his "bill-pointing" posture to the outside, the male creeps backwards toward the female, his throat lowered onto the log, rapidly flapping his wings alternately, flashing his white wing-patches. He approaches the female until she either touches him with her bill or flies off. (4) The male returns to his perch, in line with the log. (5) The male again performs the display flight with synchronous calls. (6) Immediately after having snapped his wings and landed in bill-pointing posture to the outside, the male drops to the female's back for copulation.

by dropping to the log, snapping the wings, and performing an about-face above the female. The male lands beyond the female with a snap of his wings (producing the "pop," Prum 1986) and rebounds toward the outside over the female. The male then walks backwards toward his partner, head down and tail up, opening his wings alternately ("slow undulating crawl," Davis 1949; "wing-shiver display," Prum 1986). The throat feathers are raised by rubbing them against the moss, the primary remiges and the rectrices pointing toward the female's head (Fig. 4). I observed 168 courtship displays by solitary males in the presence of a female. These courtships were very stereotyped and the male always performed the display call ending in a final "pop." On 128 occasions, the male landed in "bill-pointing posture" after the rebound over the female. On 40 occasions, the male began the "wing-shiver display" immediately upon the second landing. During the three displays resulting in copulation, the female touched the tips of the male's primaries with her bill at the end of the "wing-shiver display." This behavior, also observed in *Pipra erythrocephala* (Lill 1976), *P. filicauda* (Schwartz and Snow 1978), and *Rupicola rupicola* (Snow 1971) probably indicates acceptance of copulation. The male then repeats the display, starting from the ritualized display flight, and lands directly on the female after dropping to the log, snapping his wings, and performing an about-face. During the same breeding season, two copulations were performed by two different banded males using different fallen logs on the same arena. This evidence does not support the "hotshot model" of lek evolution (Beehler and Foster 1988), because different males from the same arena seemed to be equally attractive for females.

Quite obviously, the mobile group display is less important in White-throated Manakin's breeding system than exclusive territorial behavior. In my observations, the log-approach displays differ when performed competitively from when they are performed during a female visit. The white throat-patch is directed inward for competitive displays in the absence of

FIG. 4. Adult male *Corapipo gutturalis* "wing-shiver display" in front of a female. Walking backwards, the male rubs his throat against the moss-covered log and opens his wings alternately, displaying the three white patches in his plumage. To signal acceptance of copulation, the female touches the tips of the primary remiges with her bill.

a female (Fig. 2) and outward for female courtship with "wing-shiver display" (Fig. 3). However, competitive displays certainly have an attractiveness function in courtship behavior, since Davis (1949) observed a pair copulate immediately after a group display. Despite intensive searching I never observed or heard any flight-song display of White-throated Manakins above the forest canopy as described by Davis (1982) and Prum (1986). On the other hand, I observed on 35 occasions a different form of log approach in which a male flew from a nearby perch to the log in a slow flapping "butterfly flight." The wingbeat was very deep and so slow that the white wing-patches were clearly visible at each downstroke of the wing. This log approach, which performance by solitary males (N = 12) or by residents in reaction to the visit of neighboring males (N = 23) was only observed during the breeding season, is very similar to the display flight of White-crowned Manakins (Snow 1961, pers. obs.).

In French Guiana, the 31 display logs located were organized in five exploded leks (two on the "Piste de St-Elie" site and three on the "Inselberg des Nouragues" site). The mean distance between display logs of each arena was 38 ± 13 m (N = 26). Leks were about 120 m in diameter and 230 m apart. Prum (1986) found in Suriname a similar spatial organization of the display sites, even if the "exploded" leks were significantly larger and farther apart (about 250 m in diameter and 350 m apart). However, Prum (1986) concluded the existence of a "detached" or "mobile" lek was due to "the abandonment of exclusive display territories for the competitive group display at a series of sites." I agree with Davis (1949) and Prum

(1986) that females White-throated Manakins sometimes choose to visit males during group display, but I consider exclusive territorial behavior to be more important in this species breeding system than mobile group display. My observations of three copulations after single male's displays show that group display is not an absolute condition for copulation to take place. Consequently, I consider White-throated Manakins to be simply organized in "exploded" type leks.

Adult *Corapipo gutturalis* males, like *Manacus manacus* and *Pipra erythrocephala* males, occupy territories which, at set display times, benefit from better lighting conditions with respect to the surrounding areas (Théry 1987). In *Pipra serena,* the daily variations of light exposure in the understory could lead to the regular movement of males in a "double-spot lek." The type of lek used by different species (classic or exploded, single- or double-spot) may be determined in part by environmental conditions (spatial and temporal distribution of food resources, availability of appropriate display sites) as well as by size of the ranges of the males and females.

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Lead concentrations in Golden and Bald eagles.—In recent years, lead (Pb) was found in elevated concentrations in free-ranging Bald Eagles (*Haliaeetus leucocephalus*), sometimes in high enough quantities to cause mortality (Kaiser et al. 1980, Reichel et al. 1984). Published reports of mortality due to lead poisoning in other free-ranging raptors are few. California Condors (*Gymnogyps californianus*), Rough-legged Hawks (*Buteo lagopus*), Golden Eagles (*Aquila chrysaetos*), and a Red-tailed Hawk (*Buteo jamaicensis*) have died due to lead poisoning (USFWS 1985, Wiemeyer et al. 1988). Additionally, other Golden Eagles which died from diseases or unknown causes contained elevated lead concentrations (USFWS 1985). We report lead concentrations in the livers of 16 Golden and six Bald eagles and in blood samples from two Golden and two Bald eagles found dead or moribund in Idaho.

Study area and methods.—From 1977 through 1984, the Idaho Department of Fish and Game (IDFG) sent eagles to the National Wildlife Health Research Center (NWHRC),

TABLE 1

FREQUENCY DISTRIBUTIONS AND MEANS OF LEAD CONCENTRATIONS IN LIVERS FROM BALD AND GOLDEN EAGLES COLLECTED IN CENTRAL AND SOUTHERN IDAHO, 1977–1986

Species	N	$\bar{x}$ (SD)[a]	Frequency distribution (ppm wet wt.)		
			<2.0	2.0–8.0	>8.0
Golden Eagle	16	8.86 (9.02)	7	2	7
Bald Eagle	6	25.70 (17.04)	1	0	5
Total	22		8	2	12

[a] Standard deviation in parentheses.

Madison, Wisconsin, for necropsy if the cause of death was not apparent. After learning that some of these eagles died of lead poisoning, the IDFG made a concerted effort during 1985 and 1986 to send eagles that they obtained in central and southern Idaho to the NWHRC for necropsy.

Habitats in central and southern Idaho vary from flat to rolling, cool desert dominated by sagebrush (*Artemisia tridentata*)-grass associations to mountainous areas containing major river systems. Vegetation changes with elevation from cool desert to subalpine.

Lead concentrations in liver were determined by the NWHRC following necropsy. In addition, one blood sample from a live Bald Eagle was sent to the NWHRC for analysis. Five ml blood samples were taken by brachial puncture and sent to the Washington Animal Disease Diagnostic Laboratory, Washington State Univ., Pullman, Washington for analysis from an additional three sick birds (two Golden Eagles and one Bald Eagle). All samples were reported on a wet weight basis (minimum detection level = 0.10 ppm) as are all literature values reported herein.

Results and discussion.—Five Golden Eagles and one Bald Eagle were recovered from 1977 to 1984. Eleven Golden Eagles and four Bald Eagles were recovered in 1985 and 1986, and one Bald Eagle was recovered in 1987. In addition, blood samples were collected from two live Bald Eagles and two Golden Eagles in 1985 and 1986. Both a liver and a blood sample are reported for one of the Golden Eagles. Lead concentrations in livers of Golden Eagles ranged from 0.19 to 26 ppm and in Bald Eagles from 0.19 to 51 ppm. A greater proportion of Bald Eagles (83%) had elevated (>8.0 ppm) concentrations of lead in liver than Golden Eagles (44%) (Table 1).

Pattee et al. (1981) suggested that Bald Eagles with lead concentrations in liver >10 ppm were acutely exposed whereas NWHRC has suggested that 8.0 ppm lead in liver be used as the threshold level in Bald Eagles (letter on file). Feierabend and Myers (1984) considered Bald Eagles with lead concentrations in liver between 2.0 and 10.0 ppm to be sublethally poisoned and concentrations below about 2.0 ppm to be uncontaminated.

Five of 16 Golden Eagles and five of six Bald Eagles were confirmed by NHWRC to have died of lead poisoning. The liver of one Golden Eagle had a concentration of 16 ppm lead, although a blood sample taken 9 days before its death contained only 0.54 ppm lead. This bird died of lead poisoning and aspergillosis. Feierabend and Myers (1984) considered Bald Eagles with >0.6 ppm lead in blood to be sublethally poisoned.

Two other Golden Eagles with elevated concentrations of lead in their livers were necropsied in Idaho. One contained an apparently ingested #7½ lead shot pellet in the lower gastrointestinal tract, and the other contained a fragment of a copper-jacketed lead bullet in its proventriculus. The birds were sent to the NWHRC for secondary examination; their

livers contained 23 and 18 ppm lead, respectively. However, lead poisoning could not be confirmed because of the previous necropsy.

Waterfowl which carry embedded pellets are frequently the pathway of lead exposure to raptors (Pattee and Hennes 1983). However, a wild California Condor, which died of lead poisoning, contained a fragment of a copper-jacketed lead bullet in its gizzard (Wiemeyer et al. 1988). Neither projectile (#7½ shot or rifle bullet) recovered from the two eagles in our study area are associated with waterfowl hunting. Platt (1976) found lead pellets in castings of Bald Eagles in Utah and thought that the birds were eating hunter-killed black-tailed jackrabbits (*Lepus californicus*). We suggest that in both instances, hunter-killed game other than waterfowl may have been the source of exposure to the two Idaho eagles.

Another Golden Eagle, collected in east-central Idaho, was sublethally poisoned by lead. Its liver contained 6.3 ppm lead, and the NWHRC suggested that lead may have contributed to its death which resulted primarily from necrotic colitis (NWHRC, letter on file).

Three morbid eagles contained elevated concentrations of lead in blood samples, but X-rays revealed no lead projectiles in the birds' gastrointestinal tracts. One, an immature Bald Eagle, which exhibited symptoms of lead poisoning (ataxia, convulsions, anorexia, and absence of trauma) had 0.14 ppm lead in blood, suggesting past exposure (E. Stauber, pers. comm.). The blood sample from another Bald Eagle (age unreported) contained 0.23 ppm lead. The third bird, a Golden Eagle, was suffering from malnutrition and had an injured wing. No symptoms of lead poisoning were apparent in this bird, but a blood sample contained 0.21 ppm lead. Concentrations of 0.1 ppm or less are expected in uncontaminated birds (Feierabend and Myers 1984).

East-central Idaho is a historic lead mining and milling area. However, Custer et al. (1983) have suggested that lead poisoning in wild raptors is probably not due to ingestion of biologically incorporated lead (e.g., an eagle eating an animal whose flesh was contaminated by feeding on plants growing on tailings at a lead mine).

Relatively large populations of wintering Golden and Bald eagles and nesting Golden Eagles inhabit parts of southern Idaho (Craig et al. 1984). The nesting areas and migration routes of these Bald Eagles are not well known, although band recoveries indicate a direct southerly route from northern nesting areas to Idaho for some (USFWS 1985). Data on the migration routes of Golden Eagles wintering in eastern Idaho are lacking. Because symptoms of lead poisoning may be delayed following ingestion (Hoffman et al. 1981), eagles can travel extended distances before indications of poisoning occur. Therefore, the source of lead contamination in Idaho eagles is not known.

Ten of the 17 Golden Eagles and seven of the eight Bald Eagles examined during this study were exposed to lead. These data suggest that both species may frequently be exposed to lead, sometimes to lethal concentrations, and that lead poisoning in Golden Eagles may be a more serious problem than previously thought. However, our results may be biased because all eagles analyzed were either sick or dead. Further study is needed to determine the portion of the eagle populations in Idaho which suffer lead contamination.

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Body temperatures of migrant accipiter hawks just after flight.—Body temperature (T_b) during flight or shortly after flight has been recorded in many studies. Red-tail Tropicbirds (*Phaethon rubri cauda*) captured within 10 sec of returning to land from extended flights had a mean T_b of 40.9°C, almost 2°C higher than the mean for these birds during incubation (Howell and Bartholomew 1962). Platania et al. (1986) measured T_b of 250 seabirds of 23 species within two min after shooting the birds from a boat 30 to 60 km off the coast. The T_b of these birds flying at sea was about 1°C higher than that of individuals studied at nesting sites. Rock Doves (*Columba livia*) shot immediately after landing at air temperatures (T_a) ranging from 13 to 26°C had body temperatures between 41.5–43.8°C (Pearson 1964), and Hart and Roy (1967) measured a T_b of 44.5°C on pigeons during free flights at air temperatures between 4–30°C. The T_b of pigeons flying in a wind tunnel increased 1.5–3.0°C in the first min of flight and remained at this higher level (Hirth et al. 1987) and at T_a above

25°C ranged from 43.3 to 44.1°C (Aulie 1971, Butler et al. 1977). White-necked ravens (*Corvus cryptoleucus*) (Hudson and Bernstein 1981) and Budgerigars (*Melopsittacus undulatus*) (Aulie 1971) flying in wind tunnels had steady-state body temperatures of 43.5–44.8 and 42.1°C, respectively. In all cases during flight, the birds had a body temperature of 1–4°C above resting level.

We are not aware of any literature on the T_b of birds recorded during migratory flight or at the end of a long distance migratory flight. Hoffman's (1985) study of raptor migration along the Goshute Mountains in Nevada provided an opportunity to record body temperatures of migrating accipiters shortly after they were trapped.

Accipiters migrating along the Goshute Mountain Ridge spend much more time soaring or sailing than in active flapping flight. Since energy metabolism during soaring flight is 1/4 to 1/6 of that during flapping flight (Bartholomew 1982), we hypothesized that migrating accipiters would have a body temperature slightly below that observed for birds during continuous active flapping flight in a wind tunnel or in the field.

Methods.—We trapped Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*) in bownets and mist nets on the ridgetop (elev. 2740 m) at the southern end of the Goshute Mountains, Elko County, Nevada, in September 1983, 1984, and 1985. We measured body temperatures with glass thermometers (Schulthesis and baby rectal thermometers) or a Wescor TC Thermometer (Model TH 50; with a Cu/Con thermocouple). All temperature sensors were calibrated with a precision mercury-in-glass thermometer. We inserted a temperature sensor 1.5 cm into the cloaca; T_b was recorded when temperature reached a steady value (usually within 20 sec). We removed birds from the bownet before inserting the sensor. The T_b of some birds entangled in the mist net was measured before removing them from the net. We removed other birds quickly from the net, and then measured their T_b. The time between trapping a hawk and reading its cloacal temperature averaged 90 sec. When the elapsed time exceeded 4 min, the T_b was not included in this analysis. Data were analyzed with a general linearized model and LSD test using a SAS/STAT program for personal computers.

Results and discussion.—The mean T_b (± SD) of Sharp-shinned Hawks (40.6 ± 1.1°C) was significantly higher ($P = 0.006$) than that of Cooper's Hawks (40.2 ± 0.9°C) (Table 1). Differences of T_b between the sexes and between adults and immatures were not significant ($P = 0.221$ and 0.769, respectively). The higher T_b of the smaller species might be interpreted in two ways: (1) that an inverse relationship between T_b and body size is real, or (2) that the T_b of the smallest birds increased relatively more during the first 90 sec of capture, generating an apparent but false difference in T_b between large and small birds which did not exist at the time of capture.

In an unpublished study, we recorded rates of metabolism of accipiters 30 to 60 min after capture. The birds were confined inside loosely fitting cans. Typically, rates of metabolism were 1.5 × BMR (BMR was calculated from an allometric equation for Falconiforms [Wasser 1986]), but a few measurements were as high as 5 × BMR. These findings suggest that the metabolic rates during the first 90 sec of captivity are probably elevated in response to the stress of capture. When metabolic heat production is greater than heat loss, the difference is stored in the body, causing an increase in T_b.

We calculated two estimates of the potential increase of T_b by assuming two levels of metabolic heat production ($\dot{H}_m$) during the first 90 sec after capture: (1) 2.0 times BMR and (2) 4 times BMR (Table 2). In both cases we assumed that heat loss ($\dot{H}$) equaled the BMR of an Accipiter perched at rest. Therefore, in these two cases, the ratios of $\dot{H}_m$:$\dot{H}$ were 2 and 4. When the rate of metabolic heat production is twice the rate of heat loss, the T_b of the smallest and largest Accipiters would increase 0.17°C and 0.10°C, respectively in 90 sec (Table 2). If $\dot{H}_m$:$\dot{H}$ were 4, these values would increase by three times. The increase in T_b is less in larger birds since weight-specific metabolism decreases with increasing body mass.

TABLE 1

MEAN (±SD) POST-FLIGHT BODY TEMPERATURES OF MIGRATING SHARP-SHINNED AND COOPER'S HAWKS RECORDED 90 SEC (MEAN) AFTER BEING TRAPPED

Species	Sex		Body temperature (°C) By age: Immature T_b (N)	Mean body mass (g)	Adult T_b (N)	Mean body mass (g)	By sex: T_b (N)	By species: T_b (N)
Sharp-shinned Hawk	M		40.9 ± 1.2 (49)	97	40.0 ± 0.0 (2)	101	40.9 ± 1.1 (51)	40.6 ± 1.1 (160)
		Range	(38.2–43.6)					
	F		40.3 ± 1.0 (86)	164	40.7 ± 1.0 (23)	172	40.4 ± 1.0 (109)	
		Range	(37.6–43.5)		(39.4–42.7)			
Cooper's Hawk	M		40.3 ± 0.9 (24)	270	40.9 ± 1.6 (8)	280	40.4 ± 1.1 (32)	40.2 ± 0.9 (118)
		Range	(38.7–42.8)		(38.0–42.5)			
	F		40.1 ± 0.9 (46)	419	40.1 ± 1.1 (32)	443	40.1 ± 0.8 (86)	
		Range	(38.0–42.6)		(38.7–42.5)			

TABLE 2

PREDICTED BODY TEMPERATURE INCREASE (ΔT_b) OF ACCIPITER HAWKS IN 90 SEC WHEN THE RATIO OF THE RATE OF METABOLIC HEAT PRODUCTION (H_m) TO RATE OF HEAT LOSS (H) IS 2 AND 4

Species	Sex	Avg body mass (g)	$\dot{H}$[a] (W)	T_b (°C) when $\dot{H}_m$:$\dot{H}$ equals[b]	
				2	4
Sharp-shinned Hawk	Male	97	0.6469	0.17	0.52
	Female	164	0.9054	0.14	0.42
Cooper's hawk	Male	270	1.2457	0.12	0.36
	Female	419	1.6502	0.10	0.30

[a] $\dot{H} = \dot{H}_b = m\ (34.62\ m^{-0.36})/1000$, $\dot{H}$ is rate of heat loss in W, $\dot{H}_b$ is basal metabolic rate and m is body mass in g (modified from Wasser 1986).

[b] $T_b = 90s \cdot \dot{H}_s/c \cdot m$, where c = specific heat (=3.47 $J \cdot g^{-1} \cdot °C^{-1}$; Bligh and Johnson 1973); $H_s = H_m - H$, where H_s is rate of heat storage in W and $\dot{H}_m$ is rate of metabolic heat production for 90 sec after capture (either 2 or 4 times $\dot{H}_b$).

The difference in mean T_b observed between Sharp-shinned and Cooper's hawks was 0.4°C. It is unlikely, but possible, that this difference could have occurred during the first 90 sec of captivity, since a difference of 0.5°C would result from the most extreme case shown in Table 2 (i.e., when the $\dot{H}_m$:$\dot{H}$ of a male SS is 4 and that of a female CH is 1). Immature male Sharp-shinned Hawks had the highest maximum T_b (43.6°C) and immature female Cooper's Hawks had the lowest maximum T_b (42.6°C). The lowest T_b recorded among immatures in each group was not correlated with the size of the bird. The average body temperature of all sex and age groups among Cooper's and Sharp-shinned hawks was less than 41.0°C. Most of the literature values for the T_b of birds during active flight are greater than 41°C, supporting our original hypothesis of a lower T_b in migrating, soaring Accipiters.

Migrating Accipiters regulated their body temperature within a range of 6°C (between 37.6 and 43.6°C). The difference between the highest and lowest T_b recorded in immatures of each species-sex group was 5.4°C (male SS), 5.9°C (female SS), 4.1°C (male CH), and 4.6°C (female CH).

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Habitats Used by Common Ground-Doves in southern Alabama.—In the United States, Common Ground-Doves (*Columbina passerina*) are distributed from California to North Carolina and sporadically farther north in the East. They are considered local, uncommon to common permanent residents in the lower third of Alabama, are rare farther north (Howell 1928, Imhof 1976), and have recently been designated a Species of Special Concern statewide (Keeler 1986).

Although some authors (Howell 1928, Bent 1932, Johnston 1964, Imhof 1976) have reported on habitats used by ground-doves, they have not quantified characteristics of those habitats. Herein, we describe quantitatively the habitats Common Ground-Doves use in southern Alabama.

Study area and methods.—We studied the lower one-third of Alabama including 24 counties in 1986 and 25 during 1987. All of these counties, with the exception of the northern three-fourths of Lee County, lie in the Coastal Plain. Community type, seral stage, percent overhead cover, percent ground cover, herbaceous vegetation height, and height and diameter breast height (dbh) of the largest tree were recorded for each site where ground-doves were observed or heard while driving 322 km of roads (as per Breeding Bird Survey routes) in each county (Jones 1988). This also was done for each differing adjacent habitat for comparative purposes. Community type and seral stage were determined by species composition and physical measurements of individual plants. Each site was classified by seral stage as forb, grass, low shrub (0.3–1 m in height); high shrub (1–3 m); low tree (3–6 m); young forest (>6 m, and 10–50 cm dbh); or mature forest (>6 m, and >50 cm dbh). For community types, habitats were classified as old field, coastal dune, agricultural field, forest, or young pine plantation. Habitat variables were assessed via the quarter-point method (Brower and Zar 1984) using a 30-m interval where possible. Otherwise, an interval was used that allowed each cardinal point to be sufficiently distant from an ecotone to

TABLE 1

HABITAT VARIABLES (MEAN ± SE) FOR SITES SAMPLED IN THE COASTAL PLAIN OF ALABAMA, 1986–1987

Year	Birds present (+, −)	Overhead cover (%)	Ground cover (%)	Vegetation height (m)	Tree height (m)	Dbh (m)
1986	+	13.1 ± 5.7[a]	76.0 ± 7.2[a]	0.8 ± 0.1[a]	8.3 ± 2.0[a]	0.1 ± 0.03[a]
	−	55.2 ± 8.5[b]	68.4 ± 11.1[a]	0.9 ± 0.2[a]	23.9 ± 2.7[b]	0.3 ± 0.03[b]
1987	+	15.8 ± 3.9[a]	76.6 ± 3.9[a]	0.6 ± 0.03[b]	4.1 ± 0.4[c]	0.1 ± 0.01[a]
	−	59.3 ± 4.4[b]	70.4 ± 4.9[a]	0.6 ± 0.05[b]	18.6 ± 1.1[d]	0.4 ± 0.02[b]

[a, b, c, d] Means within a column sharing a letter are not different ($P > 0.05$).

preclude influence by canopy cover. Standard procedures used in measuring each variable have been previously described (Jones 1988).

Means of all habitat variables were grouped by the presence or absence of ground-doves (site type). Analysis of variance (ANOVA) was used to determine if any site type differences ($P < 0.05$) occurred between variables (Steel and Torrie 1980, SAS Institute Inc. 1985). Years were pooled to make comparisons between site types where there were no ($P > 0.05$) year-type interactions.

Soil characteristics, including percentage of sand, clay, silt, natural fertility, and reaction (pH), were obtained for all sites with ground-doves in eight counties in which a U.S. Soil Conservation Service (SCS) County Soil Survey existed.

Results and discussion.—Seventy sites having ground-doves were used in the analysis of habitat data. Differing but associated sites (N = 150) were used for comparative purposes. Sixty-nine sites with ground-doves were classified by habitat type as old field (31), young pine plantation (23), forest (7), agricultural field (4), coastal dune (3), and homesite (1). Ground-doves were observed in all vegetative zones from the foredunes through the hind-dunes at sites in coastal dune habitats. They also were observed in freshly plowed or recently harvested agricultural fields, and in hardwood and pine forest types. Old fields were used most often (45%), but young pine plantations also were used heavily (33%).

Overhead cover, tree height, and dbh were the only three variables found to differ ($P < 0.0001$) between site types (Table 1). Differences existed between site types ($F = 24.6$, df = 3, $P = 0.0001$) and overall year effect ($F = 13.3$, df = 3, $P = 0.0001$), with the latter attributable to the differences in sample sizes between years. No ($F = 0.6$, df = 3, $P = 0.63$) interaction between year and type existed, so years were combined and re-analyzed. In general, the canopies of sites with ground-doves were much more open ($\bar{x} = 15.14 \pm 3.3\%$ closure) than those without doves ($\bar{x} = 58.45 \pm 3.9\%$ closure). Ground cover and herbaceous vegetation height were very similar between site types. Both tree height and dbh showed trends similar to overhead cover. Sites with doves had smaller trees and dbhs (height $\bar{x} = 5.20 \pm 0.6$ m, dbh $\bar{x} = 0.10 \pm 0.01$ m) than those without doves (height $\bar{x} = 19.59 \pm 1.1$ m, dbh $\bar{x} = 0.34 \pm 0.02$ m).

Ground-doves located during this study occurred most often in early successional stages such as old fields and young pine plantations. The physical structure of these habitat types, rather than the species composition, seemed most important. The Common Ground-Dove has been described as a "disturbance species" (J. L. Landers pers. comm.) and would be expected to occur more frequently in the early successional habitats observed in this study. These habitats satisfy their food and nesting requirements because forbs and grasses that

produce small seeds, a major food of ground-doves, are generally abundant there. Early seral stages also provide good nesting cover (Landers and Buckner 1979).

Forty-two soil types occurred in the sample of 63 sites with ground-doves (some sites contained more than one soil type). Of the 63 sites occupied by ground-doves that could be categorized by soil type, four were sands, 26 were loamy sands, 32 were sandy loams, and one was loam. Of the 1,722,593 ha of soil types that existed in all counties, 1.12% was sand, 21.4% loamy sand, 31.9% sandy loam, and 0.97% loam. Soil characteristics of habitats in which ground-doves were found during this study were sandy soil (≥64% of content in 98.4% of sites) low pH (4.75–6.7), and low natural fertility. Sandy soils have been reported as characteristic of ground-dove habitat (Hopkins 1958). All of these characteristics probably combine to retard the rate of succession and make suitable ground-dove habitat available for longer periods of time.

The characteristics of the habitats used by ground-doves in this study support the premise that they are closely associated with early seral stages and sandy soils. Additional research to determine the exact habitat requirements of Common Ground-Doves is required. Such work should include determination of habitat requirements in other portions of the Common Ground-Dove's range and specific use(s) of each habitat.

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The seabirds of Las Islas Revillagigedo, Mexico.—Las Islas Revillagigedo comprise three volcanic islands (Socorro, Clarion, and San Benedicto, in decreasing order of size) and a rocky islet (Roca Partida). The archipelago lies in the tropical Pacific between 365 and 620 km south and southwest of the tip of Baja California. Most visitors have concentrated on the endemic landbirds, and data concerning the diverse and abundant seabirds are few. Brattstrom and Howell (1956) discussed the status of the birds on the Revillagigedos in 1953 and summarized the data of the few earlier visitors (Grayson 1872, Anthony 1898, Townsend 1890, Kaeding 1905, McLellan 1926). Jehl and Parkes (1982) reported new observations from Socorro and San Benedicto. Everett (1988) mentioned some records from Clarion in 1986.

During a cruise in February 1988, we visited all three islands and Roca Partida as follows. San Benedicto (19°18′N, 110°49′W) 9–11 February; Socorro (18°47′N, 110°58′W) 11–17 February; Roca Partida (19°00′N, 112°04′W) 18 February; and Clarion (18°22′N, 114°45′W) 19–22 February.

San Benedicto is still uninhabited by people, and we saw no introduced predators. A major volcanic eruption in 1952 radically altered the island and extirpated the two resident landbird species, but most seabirds have successfully recolonized. Due to the difficult nature of access, our observations were restricted to that portion of the island north of the saddle between the two volcanoes. However, the slopes of the 1952 (southern) volcano appeared almost devoid of life although a few boobies may have been nesting in the crater.

Socorro hosts a naval garrison as well as large numbers of introduced sheep (estimated by residents at 3000 animals), cats, and mice. More seabird species roost on Socorro than breed there, and by cruising around the island, we counted all roosting and visibly breeding seabirds.

We arrived at Roca Partida at about first light (0550), and with the probable exception of frigatebirds and perhaps noddies, we made an accurate census of the roosting birds. By 0715, only 30% of the initial number of birds remained on or about the rock.

Clarion, the remotest and least well-known of the Revillagigedos, was granted freedom from permanent human habitation until 1979 when a small naval garrison was established. Feral rabbits are now abundant on the island, as well as undetermined numbers of feral pigs (50+), chickens, and at least two sheep. We were able to census most of the island but did not reach the eastern end; however, much of this was surveyed from sea and most seabirds were probably detected.

Laysan Albatross (*Diomedea immutabilis*).—At least 11–14 were present on San Benedicto, including three displaying pairs and one bird that strongly defended an empty nest scrape. We saw one gliding over the cliffs at Cabo Henslow, Socorro, on 16 February. At least 30 birds were on land at Clarion, including two birds photographed on eggs and 12 displaying pairs.

Wedge-tailed Shearwater (*Puffinus pacificus*).—None was seen during two weeks in the Revillagigedos despite the fact they are known to breed on San Benedicto.

Townsend's Shearwater (*Puffinus auricularis*).—We saw 11 a few km from the northern end of San Benedicto but saw no nesting burrows on the island. We counted 32 between San Benedicto and Socorro. In the late afternoons of 15 and 16 January, up to 550 staged 1–4 km off the northwest side of Socorro. Eighty-one flew north and northeast as we approached Clarion. On land, all nesting sites were marked by severe pig rooting, and numerous shearwater remains littered the destroyed burrows. We found no occupied burrows.

Red-billed Tropicbird (*Phaethon aethereus*).—We counted 50–70 pairs at San Benedicto. At least seven birds were seen in, entering, or leaving crevices, but the majority were engaged

in courtship flights and nest prospecting. This species was present on Socorro as follows: 5–6 pairs courting and prospecting along the cliffs at Cabo Pearce and two pairs courting over Roca Oneal. At Clarion, we counted 40–50 pairs. The main concentrations were at the eastern end of the island (40+ birds) and along the northwest cliffs (42+ birds). Many birds engaged in courtship flights, and the breeding season seemed at a similar stage to that on San Benedicto.

Red-tailed Tropicbird (*Phaethon rubricauda*).—On San Benedicto we observed and photographed 2–5 birds, including 1–2 pairs in courtship flights. One pair made repeated landing passes at a cliff face near the northwest corner of the island, strongly suggesting the species was to breed there.

Masked Booby (*Sula dactylatra californica*).—On San Benedicto we estimated 585–600 pairs on territory. Of 59 nests, 34 had chicks and 25 had eggs but our overall impression was that about 70% of pairs had young. The majority (65%) nested on the floor of the old crater. We also photographed four individuals with the deep orange bills and gray feet characteristic of *S. d. granti*, the Galapagos subspecies. Two were attending chicks, and at least one was paired with a *californica*. We saw 40–50 adults on Roca Partida and the main group, all *californica*, soon headed out to sea. However, four birds remained (all *granti*), three on the south pinnacle (including a displaying pair) and one on the north. The minimum population of Masked Boobies at Clarion was 380–470 pairs at five sites. Many were displaying, but none appeared to be on eggs. Three *granti* were seen at two sites, but many birds were too distant for subspecific determination.

Red-footed Booby (*S. sula*).—On San Benedicto, we found two colonies, one of 50 nests and the other of four nests. The larger colony included 35 birds on eggs, nine with small chicks, three fledglings, and three juveniles. Of 36 adults at nests, 35 were white morph and one brown. Tail color of the 35 white morphs at nests varied; six had white tails, 14 intermediate, and 15 black. One brown and three white adults were at the second site, plus four recently fledged juveniles. We did not visit the lava delta where Jehl and Parkes (1982) reported a Red-footed Booby colony. Two immatures roosted with the Brown Boobies on Socorro, 16 February. On Clarion there were 3010–3210 pairs at five sites, all on the eastern half of the island, the largest colony being 1500–1600 pairs. 60–70% of the nesting birds had a single egg, the rest had empty nests. We saw one dead newly hatched chick. Ninety-nine percent of the adults were white morphs, 0.5% brown morphs and 0.5% intermediate. Of the white morphs, 85–90% were black-tailed, 5% intermediate, and only 5% white-tailed.

Brown Booby (*S. leucogaster*).—We counted 45–50 pairs on San Benedicto, all but one scattered on the slopes of the valley below the raised northern part of the island. Of 41 nests examined, 21 had young and 20 had eggs. At least 30–40 recently fledged juveniles were flying around the island, and we suspect the actual breeding population was closer to 75–100 pairs. On Socorro, up to 120 birds roosted along the cliffs between Grayson Cove and Cabo Henslow. At Roca Partida, the total of 320–350 included 12–15 immatures, 25–30 juveniles, and at least 20 displaying pairs. By 0630, only 140 birds remained on the rock. At Clarion, we saw at least two adults on the island and suspect a few pairs may nest at the eastern end.

Great Frigatebird (*Fregata minor*) and Magnificent Frigatebird (*F. magnificens*).—On San Benedicto, we photographed both species nesting together in a north-facing valley near the northeast corner of the island. The Great Frigatebirds had nearly finished nesting: of 98+ young, only eight were guarded by adults although 48 others still had extensive white down on the head, back, and chest. The Magnificent Frigatebirds were only beginning to breed, all at the periphery of the colony: a single male and female were incubating at two nests, and a pair was courting on the ground. We saw at least 6–8 other Magnificents nearby (one male, three or four females, two or three immatures). 80–90 frigatebirds (most if not all

TABLE 1
STATUS OF THE SEABIRDS OF LAS ISLAS REVILLAGIGEDO, MEXICO

Species	San Benedicto	Socorro	Roca Partida	Clarion
Laysan Albatross	P	—	—	B
Wedge-tailed Shearwater	B	—	—	—
Townsend's Shearwater	F	B	—	B
Red-billed Tropicbird	B	B	?	B
Red-tailed Tropicbird	P	—	—	—
Masked Booby	B	—	P	B
Brown Booby	B	—	B	?
Red-footed Booby	B	—	—	B
Magnificent Frigatebird	B	?	—	—
Great Frigatebird	B	—	—	?
Sooty Tern	—	B	B	—
Brown Noddy	—	B	?	—

B—confirmed breeding; P—probable/imminent breeding (displaying/courting birds); F—formerly bred; ?—possible breeding (adults present).

Great) roosted on a steeply sloping face at the northwest corner of the island. On Socorro up to 18 Magnificents (three males, eight females, two sub-adult females, five immatures) roosted on Punta Tosca, up to six (five females, one immature) at Cabo Henslow and six (four males, one female, one immature) at Bahia Academy. The only Great Frigatebird we identified at Socorro was a female near Bahia Braithwaite, 12 February. At Roca Partida, we saw at least 15 frigatebirds, including two or three Great (one female, one to two immatures) and seven or eight Magnificent (two males, three females, one sub-adult female, one to two immatures). On Clarion, 80–90 Great Frigatebirds (10 males, 20 females, 50+ immatures) roosted on a stack at the base of the high northern cliffs. We also saw up to three or four Greats daily around Sulphur Bay but found no evidence of nesting. We identified no Magnificent Frigatebirds at Clarion.

Sooty Tern (*Sterna fuscata*).—Up to 14 associated with the flocks of Townsend's Shearwaters off Socorro but we saw none at Roca Oneal. Of 40–50 adults at Roca Partida, at least two or three probably were on eggs and several pairs were displaying.

Brown Noddy (*Anous stolidus*).—Many of the 90–100 initially present at Roca Partida left by 0630; a few remained on the southern pinnacle during our visit but none appeared to be nesting. We saw none at or near Socorro.

Discussion.—We herein clarify the status of the seabirds of the Revillagigedos. Table 1 provides a quick reference to the status of all breeding seabirds of the islands through February 1988.

Laysan Albatrosses were first recorded around the Revillagigedos when two were seen between Socorro and San Benedicto, 4 March 1979 (Pitman 1985). The next report was of three displaying behind the beach at San Benedicto, May 1987 (Pitman 1988). Everett (1988) did not see any on Clarion in January 1986 but may have missed them (W. T. Everett pers. comm.). Our data from the Revillagigedos and other sites (to be published separately), plus those of Pitman (1985) and Dunlap (1988), indicate this species is undergoing an unprecedented colonization of islands off western Mexico.

Wedge-tailed Shearwaters breed only on San Benedicto and apparently leave the island

between at least November and February. McLellan (1926) reported "thousands nesting" in May 1925. Following the 1952 eruption, Brattstrom and Howell (1956) reported Wedge-taileds as "common" in March 1953 and found their burrows in November 1953 although no birds were then present. Jehl and Parkes (1982) reported 1000 burrows in April 1978 and concluded that dark morphs comprised more than 90% of the San Benedicto population. S. F. Bailey (pers. comm.) and R. L. Pitman found the species conspicuous around San Benedicto and Socorro in mid March 1988 and, on San Benedicto, noted burrows with fresh footprints on 13 March.

Townsend's Shearwater, endemic to the Revillagigedos, breeds on Socorro and Clarion. Jehl (1982) estimated the Socorro population at 1000 pairs, but how much predation by feral cats has affected numbers is unknown. The population on Clarion has never been censused, and its existence there is threatened by pigs. Everett (1988) found "numerous unoccupied burrows" in 1986 but noted no pig rooting; presumably the pigs wait until shearwaters are on land before beginning their destruction. Small numbers bred on San Benedicto prior to the 1953 eruption (Jehl 1982), but apparently none has recolonized. We recommend the populations be censused as soon as possible and the full impact of predation evaluated.

Anthony (1898) reported Red-billed Tropicbird as "common" at San Benedicto and Clarion. McLellan (1926) reported the species as "not common on either Socorro or Clarion but . . . more numerous on San Benedicto." Brattstrom and Howell (1956) reported the species common at San Benedicto and, in March, saw three at Socorro and two at Roca Partida but none at Clarion. Jehl and Parkes (1982) reported 2–4 pairs at Roca Oneal, Socorro, and ten at San Benedicto in April 1978. Our data indicate the Red-billed Tropicbird breeds commonly on San Benedicto and Clarion and locally on Socorro. It may be only a visitor to Roca Partida which, in 1988, appeared unsuitable for nesting. Available data indicate nesting between February and November.

The only previous records of Red-tailed Tropicbird near the Revillagigedos are those of Pitman (1986). The species is known to breed no closer than Hawaii (AOU 1983), although it may breed on Clipperton Atoll (R. L. Pitman pers. comm.). Its presence on San Benedicto represents a major range extension.

The Masked Booby is known to breed on San Benedicto and Clarion. Brattstrom and Howell (1956) saw it at Roca Partida, but our observations are the first indication it might breed there. The earliest population estimates for San Benedicto are 1500–2000 nests in April 1978 and about 1000 nests in April 1981 (Jehl and Parkes 1982). Brattstrom and Howell (1956) estimated the Clarion population at 150 birds in March 1953, and Everett (1988) reported at least 200 birds "nesting" there in January 1986 but saw no eggs. Whether our counts of 600 pairs on San Benedicto and 400 pairs on Clarion represent, respectively, a true decline and increase is unclear. Interestingly, Anthony (1898) noted Masked Booby as "much more abundant" on Clarion than San Benedicto. Only one of the 1988 sites on Clarion corresponded with the three in January 1986 (W. T. Everett pers. comm.). Pigs may interfere with ground-nesting species and cause colonies to move around.

No previous observers reported *S. d. granti* on the Revillagigedos. This distinctive subspecies comprised less than 1% of the breeding Masked Boobies on San Benedicto but perhaps as much as 3% of the Clarion population. On Roca Partida, *granti* may be the only form breeding.

In recent years, the Brown Booby appears to have been the least common booby on San Benedicto. The maximum number of nests reported was only four in April 1978 (Jehl and Parkes 1982), although Anthony (1898) considered Brown about as common as Masked Booby. Our apparently high estimate, by recent standards, may simply reflect the timing of our visit. The only reference to Brown Boobys breeding at Roca Partida is of "some . . .

nesting" in March 1953 (Brattstrom and Howell 1956); its current status there is unknown though our data suggest it probably still breeds on the rock.

The Red-footed Booby breeds on San Benedicto and Clarion. For a summary of its status on the former island see Jehl and Parkes (1982); our data apparently represent the first colonies in the interior of the island since the 1952 eruption and may indicate that the vegetation has only recently returned to a level acceptable to the species. Anthony (1898) termed Red-footed "very abundant" on Clarion and McLellan (1926) reported "large colonies" there. Brattstrom and Howell (1956) reported only 150--200 birds in March 1953, which apparently led Nelson (1978:680) to state that Red-footed "used to nest abundantly . . . on Clarion." Everett (1988) counted "at least 800 active nests" on Clarion in January 1986. Our data indicate that Clarion still constitutes a major breeding ground for the species. Black-tailed white morphs have been reported only from the Galapagos (Nelson 1978:655) but made up the majority of Revillagigedo birds in 1988.

Jehl and Parkes (1982) were the first authors to report Magnificent Frigatebird from the Revillagigedos; all frigatebirds they saw on Socorro were this species, as were some on San Benedicto. Our discovery of Magnificent and Great frigatebirds nesting together on San Benedicto is the first report of their sympatric breeding away from the Galapagos. Magnificent Frigatebirds are known only to roost on Socorro, but we agree with Jehl and Parkes (1982) that the species may nest on the slopes above Bahia Academy. Our observations of Magnificent Frigatebirds are the first from Roca Partida which seems to be a roost site for wide-ranging individuals of both frigatebird species.

Great Frigatebirds have long been known to nest on San Benedicto. Brattstrom and Howell (1956) also cited nesting on Clarion (see below). In addition, Brattstrom (in Jehl and Parkes 1982) reported frigatebirds sp. nesting on Roca Partida; the habitat seems most unsuitable. Brattstrom and Howell (1956) were the first to estimate the San Benedicto population and reported 150+ birds in November 1953. Jehl and Parkes' (1982) reports of Great Frigatebirds include the following: in 1978 Pitman (Jehl and Parkes 1982) recorded 50 birds roosting on the steep slope at the northwest corner of the island, but in 1981 Jehl and Parkes reported "about 50 pairs" which were apparently nesting there. In 1988, this site was again occupied by roosting birds which we studied carefully with a telescope to ascertain that they were not nesting; the cliff seems an improbable nesting site. Our data indicate the breeding population was about 100 pairs.

Visitors to the Revillagigedos prior to Brattstrom and Howell referred all frigatebirds from the coasts of Baja California and the Revillagigedos to "*Fregata aquila*" = *magnificens*, but it has since been shown that specimens from the Revillagigedos are referrable to *minor*. Townsend (1890), the first naturalist ever to visit Clarion, reported that "large communities of these birds (*Fregata aquila*) occupy the bushes and rocks in some parts of the island and doubtless breed there." Anthony's (1898) sole comment on the species at Clarion was "Abundant," although he described in some detail the species' nesting on San Benedicto. Anthony was accompanied by Kaeding, who later (Kaeding 1905) summarized the avifauna of the Revillagigedos and stated "The frigate bird breeds commonly on San Benedicte and Clarion Island, full grown young and fresh eggs . . . being found during May." Unfortunately, no eggs or young were taken from Clarion, and all evidence for Great Frigatebird breeding on Clarion rests on Kaeding's statement. Although we see no reason why it should not breed there, we suggest that the breeding status of Great Frigatebird on Clarion should, at present, be considered hypothetical.

Both Sooty Tern and Brown Noddy reportedly breed on Roca Oneal off Socorro and on Roca Partida (Brattstrom and Howell 1956). At Roca Oneal, both have been recorded in April and May, in "large" colonies (Anthony 1898), with Brown Noddy "if anything more numerous" than Sooty Tern (Kaeding 1905). Based on our observations, some Sooty Terns

return to the vicinity in February. S. F. Bailey (pers. comm.) and R. L. Pitman saw 1000-1500 Sooty Terns at Roca Oneal, 15 March 1988 but only one Brown Noddy around Socorro, 14 to 19 March 1988.

At Roca Partida, McLellan (1926) reported a juvenile Sooty Tern on 2 May 1925 which, with our data, indicates a breeding span of at least February to May, somewhat earlier than at Roca Oneal. However, Brattstrom and Howell (1956) made no mention of either species at Roca Partida in March 1953, so breeding chronology may vary annually. McLellan (1926) also reported that Brown Noddies were "believed to be breeding" at Roca Partida, apparently the basis for the breeding cited by Brattstrom and Howell (1956). Our data also suggest Brown Noddy may breed on Roca Partida, but this is not yet proven.

In addition to the species mentioned above, Brattstrom and Howell (1956) reported "several" Blue-footed Boobies (*S. nebouxii*) from San Benedicto in November 1953, and Parkes tentatively identified one there in April 1981 (Jehl and Parkes 1982). However, the species is fairly sedentary in western Mexico (Pitman 1986, S. N. G. Howell pers. obs.), and we consider its presence at San Benedicto hypothetical.

A colony of White Terns (*Gygis alba*) has been reported from Roca Oneal, Socorro (Friedmann et al. 1950); however, the species appears to be no more than a vagrant to the Revillagigedos, as clarified by Brattstrom and Howell (1956).

Las Islas Revillagigedo constitute a unique mixing ground of seabird faunas. The preponderance of dark-tailed white morph Red-footed Boobies, the presence of *S. d. granti*, and the sympatric breeding of Great and Magnificent frigatebirds suggest the Galapagos Islands, while the newly arrived Laysan Albatross and Red-tailed Tropicbird add an element recalling Hawaii. Hopefully, future surveys can be undertaken on a more regular basis than the total of fewer than ten in the past 112 years, so that a greater understanding of the islands' seabird fauna can be achieved.

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Nearctic passerine fall migration in central Belize.—Although migration across the Gulf of Mexico is now an accepted phenomenon for many birds that breed in the Nearctic (Lowery 1951, Stevenson 1957, Buskirk 1980), little is known about specific routes, landing areas in fall (Paynter 1955, Rogers et al. 1986, Bossong 1988), staging areas in spring (Rogers et al. 1982), wintering areas, or habitat corridors for transients. Paynter (1951) estimated the minimum number of birds that arrived on the Yucatan peninsula during fall migration at over one million. Many of the species that cross the Gulf of Mexico pass through or winter on the Yucatan peninsula (Paynter 1951, 1953, 1955, Rogers et al. 1986, Bossong 1988). The landing areas for many species on the Yucatan peninsula have not been identified (Paynter 1955, Rogers et al. 1986, Bossong 1988). Therefore, we present data concerning migrant arrival times and weights during fall migration in central Belize.

We captured migrants on a citrus plantation (BGMC Limited) at mile 36 on the Western Highway, Cayo District, in central Belize, Central America (17°10'N, 88°40'W). We operated 15 mist nets (12 m × 2.6 m, 36 mm mesh) from 0600 to 1200 h during fall migration (25 August–18 November 1986). We weighed migrants with Pesola spring scales (to the nearest gram), banded each with a Fish and Wildlife Service band, and measured unflattened wing chord. Capture rates are reported as birds/net-h. The amount of fat remaining in migrants arriving in Belize was estimated by subtracting live weight from the mean fat-free weights given by Connell et al. (1960), Rogers and Odum (1964), Rogers (1965), and Hicks (1967). This region of Belize receives approximately 3500 mm of annual rainfall (129 mm during the fall study period) and is a transition zone from pine savannah to hardwood forest. The plantation is bordered by the Sibun River, and the surrounding vegetation has been described as semi-rainforest (Lundell 1945). Many areas within the plantation support successional growth, and other agricultural products are grown adjacent to the orange orchards.

We captured 1170 migrants of 47 species (0.33 birds/net-h) during fall migration, and 23 warbler species (Parulinae) accounted for 79% of the total number of individuals. Three

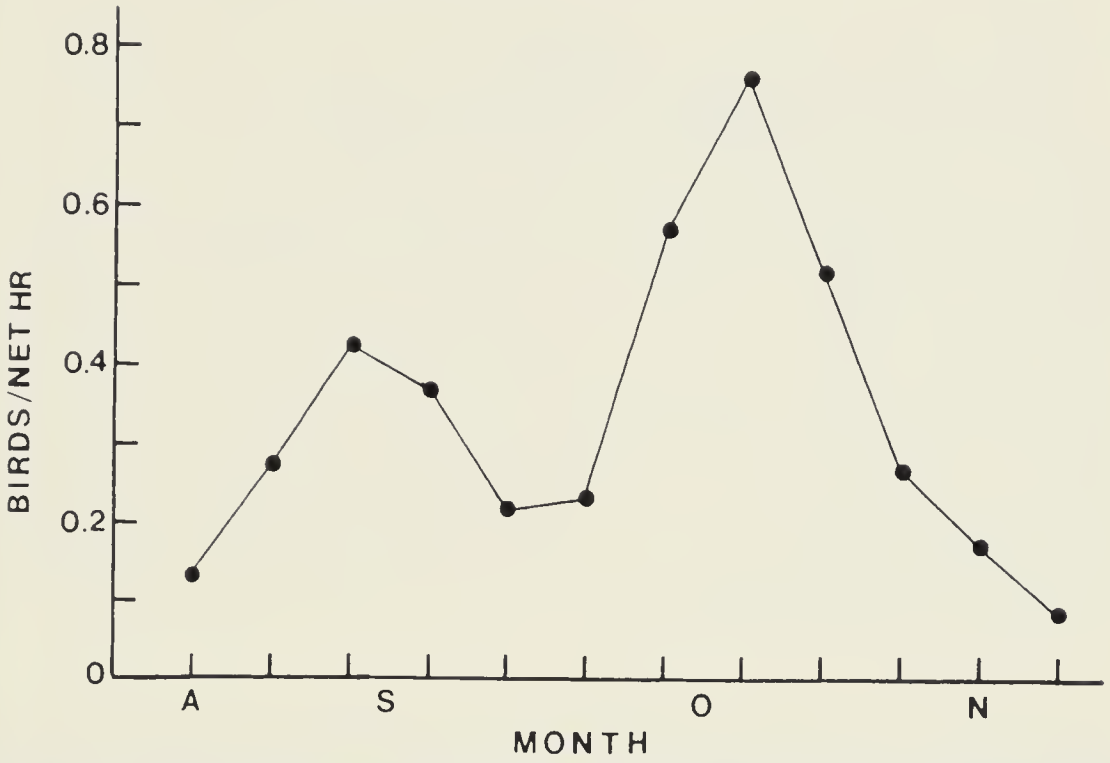

FIG. 1. Capture rates of migrants during fall migration (25 Aug–18 Nov 1986) on a citrus plantation in central Belize.

species (Magnolia [*Dendroica magnolia*], Prothonotary [*Protonotaria citrea*], and Yellow [*D. petechia*], warblers) accounted for 36% of the total number of migrants. Migrants did not arrive in a continuous stream but exhibited two peaks (Fig. 1). The first peak (8–14 Sept.) was due mainly to flocks of the transient Yellow and Prothonotary warblers. The second peak (13–19 Oct.) consisted of many species and coincides with the usual departure time of large numbers of birds from North America (Lowery and Newman 1966, Buskirk 1980). There was a dramatic increase in the number of birds arriving in Belize during the first week of October. On 7 Oct. we captured seven birds representing five migrant species, and 8 Oct. we caught 54 birds of 12 migrant species. Two cold fronts moved along the northern Gulf coast during this same week, but the weights of individuals of several species that arrived before and after these cold fronts were not significantly different (Table 1). Ovenbirds (*Seiurus aurocapillus*) had the least estimated fat, while Common Yellowthroats (*Geothlypis trichas*) were very fat (Table 2).

Lowery (1945) described the phenomenon of a coastal hiatus for spring migratory birds on the northern Gulf coast during periods of fair weather. The northern part of the Yucatan peninsula may also be an overflight zone for migrants in the fall, and mist net studies in Yucatan have shown that very few migrant species and individuals are found within 50 km of the coast (Rogers et al. 1986, Bossong 1988). There are three other lines of evidence indicating that northern Yucatan is an overflight zone : (1) Buskirk (1968) reported few fall migrants arriving in coastal Yucatan during fair weather but noted large fallouts of migrants with unfavorable southerly winds over the Gulf of Mexico. He believed they were tired from flying into a headwind. (2) We caught 10 nearctic migrant species in central Belize (450 km south of the coast of Yucatan) on dates earlier than previously recorded on the Yucatan Peninsula. Paynter (1955) and Rogers et al. (1986) reported data from a combined 120 sites in Yucatan, Campeche, and Quintana Roo. Many of our captures in this study

TABLE 1
MIGRANT WEIGHTS (MEAN GRAMS ± SD) IN CENTRAL BELIZE BEFORE AND AFTER OCTOBER COLD FRONTS, FALL 1986

Species	Before	After	*F* value[a]
Black-and-white Warbler (*Mniotilta varia*) N = 26, 74[b]	9.6 ± 1.1	9.2 ± 0.9	2.08 ($P = 0.11$)
Hooded Warbler (*Wilsonia citrina*) N = 14, 28	9.9 ± 1.2	9.7 ± 0.7	2.25 ($P = 0.10$)
Tennessee Warbler (*Vermivora peregrina*) N = 12, 55	8.9 ± 1.5	8.3 ± 1.2	2.96 ($P = 0.09$)
Northern Waterthrush (*Seiurus noveboracensis*) N = 43, 41	14.9 ± 1.5	14.6 ± 1.8	2.14 ($P = 0.15$)

[a] One-way ANOVA for unequal sample sizes.
[b] N = sample size before and after cold front.

were only one or two days earlier and might represent normal variation in the timing of fall migration. However, 2 Blue Grosbeak (*Guiraca caerulea*) was one month early, Blue-winged Warbler (*Vermivora pinus*) was over two weeks early, and Yellow-bellied Flycatcher (*Empidonax flaviventris*) was 10 days early. (3) We caught 14 migrant species that were not recorded inland by Rogers et al. (1986), Bossong (1988), or Paynter (1955) during fall migration. Some of these were noted by Paynter along the coast or on adjacent islands. These coastal reports could be the result of unfavorable weather conditions that forced migrants to land, or the differences in species composition might be due to slightly different migration patterns through the Yucatan peninsula.

From the third week in August until the first week in October 1986, there were no cold fronts along the northern Gulf coast or extending out into the Gulf of Mexico. Some studies have suggested that many migrants may wait for northerly winds or cold fronts before crossing the Gulf (Lowery and Newman 1966, Buskirk 1968, Able 1972). A cold front would provide a tailwind, allow birds to conserve energy, and reduce the chances of flying into a headwind above the Gulf of Mexico. The 1000 km flight from the coast of the United States to the Yucatan peninsula takes from 20–30 h for most passerines, depending on the weather conditions over the Gulf (Buskirk 1980). During the first week of October, two cold fronts pushed across the southern United States and extended out into the Gulf. Migrants arrived in flocks during this period, gave frequent vocalizations (calls), and made many short, rapid flights from tree to tree. This hyperactive behavior after the two cold fronts in October suggests the migrants may have landed closer to central Belize than the coast of Yucatan. The migrants that arrived before the cold fronts may have landed farther from our study site and then fed as they moved south across the peninsula. This might account for the similar weights of migrants at our study site before and after cold fronts.

Transient species arrived earlier than winter resident species, as might be expected. Migrants that typically winter south of Belize such as Prothonotary, Canada (*Wilsonia canadensis*), and Yellow warblers (*Dendroica petechia*), and Eastern Kingbirds (*Tyrannus tyrannus*) arrived in September and disappeared by October. The bulk of the wintering migrants arrived with the cold fronts in October, and remained until late April–early May 1987.

TABLE 2

ESTIMATED FAT REMAINING FOR SELECTED MIGRANT SPECIES IN BELIZE, FALL 1986

Species	Weight ± SD	Fat (g)
Swainson's Thrush (*Hylocichla ustulata*) (N = 11)	28.4 ± 2.3	2.9
Gray Catbird (*Dumetella carolinensis*) (N = 9)	34.4 ± 2.3	2.6
Tennessee Warbler (*Vermivora peregrina*) (N = 67)	8.4 ± 0.9	0.9
Prothonotary Warbler (*Protonoteria citrea*) (N = 128)	12.6 ± 1.3	1.6
Magnolia Warbler (*Dendroica magnolia*) (N = 161)	7.1 ± 0.8	0.4
Ovenbird (*Seiurus aurocapillus*) (N = 29)	16.4 ± 1.2	0.4
Northern Waterthrush (*Seiurus noveborarensis*) (N = 84)	14.8 ± 1.6	0.8
Common Yellowthroat (*Geothlypis trichas*) (N = 32)	9.7 ± 0.8	1.3
Summer Tanager (*Piranga rubra*) (N = 8)	28.2 ± 2.1	3.1
Indigo Bunting (*Passerina cyanea*) (N = 31)	13.1 ± 1.3	1.0
Orchard Oriole (*Icterus spurius*) (N = 6)	19.8 ± 1.5	1.7

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The location of the Mexican locality, Valle Real.—From 1824 to 1829, Ferdinand Deppe and his companions were the first naturalists to collect birds in Mexico for scientific purposes (Stresemann 1954). During this period, Deppe visited a locality, then known as Valle Real, where he collected a number of bird specimens, some of which were used by various authors as types of new species or subspecies. This locality has been referred almost universally to as the state of Veracruz (e.g., Ridgway 1914:356–357, 486; Stresemann 1954; Miller et al. 1957:14, 23). Some years ago, F. W. Loetscher, Jr. (in litt.) suggested to me that Valle Real might be synonymous with Valle Nacional, Oaxaca, a supposition with which I concurred but could not confirm (Binford 1989:389). Recently, however, I discovered an old map that, together with other data, proves this to be the case.

The map (Fig. 1), entitled "Mapa de Departamento Oaxaqueño," was prepared by Juan B. Carriedo and dated 1840. It shows a nearly direct trail from "Oajaca" [=Oaxaca City] through "Capulalpa" [Capulalpan], "Yxtlan" [Ixtlán de Juárez], Jaltianguis, Analco, Comaltepec [Santiago Comaltepec], "Yolos" [San Pedro Yolox], Guajimulco [probably Santiago Cuanimulco], "S. Juan" [probably San Juan Quiotepec], "Etla" [probably San Mateo Yetla], "Valle real" [Valle Nacional], "Tustepec" [San Juan Bautista Tuxtepec], and "Otatitlan" [Otatitlán, Veracruz] to "Chalcatiangis" [Chalcatianguis, Veracruz]. The last town is on the Río Papaloapan, which flows past "Cosamaluapa" [Cosamaloapan; Fig. 1D] to the Gulf of Mexico at Alvarado, Veracruz. Although these 16 towns are not in the exact positions shown on modern maps, they are located properly in relation to one another. Most importantly, "Valle real" (Fig. 1A) is between "Yolos" (B) and "Tustepec" (C), approximately where

modern maps place Valle Nacional. Thus, "Valle real" on the 1840 map is synonymous with present day Valle Nacional. It is situated along the Río Valle Nacional in the Atlantic lowlands at the foot of the Sierra de Juárez. Its elevation is 65 m, and its coordinates are about 17°47′N latitude, 96°18′W longitude, 42 km southwest of San Juan Bautista Tuxtepec.

Another Oaxaca map in my possession, dated in the 1880s, uses the name "Valle nacional." Thus, the name was changed, at least on maps, between 1840 and 1890. Because "real" in Spanish can mean "royal" or "royalist" in addition to "beautiful," perhaps the change was made for nationalistic reasons after the Mexican revolution. The use of small letters beginning "real" and "nacional" has no special significance; adjectives often were not capitalized, even in place names.

That this Valle Real is the one visited by Deppe is confirmed by the following. Deppe's travels in Mexico, based on his letters and on entries in Hinrich Lichtenstein's lists of specimens, both in the Berlin Museum, are outlined in Stresemann (1954:87). Deppe left Oaxaca City on 6 December 1825 "and chose a direct route to Alvarado which proved very difficult. On December 18, he crossed the Cordillera Costal at a place called Valle Real, Veracruz, clad with luxuriant forest in which, besides many fine birds, a troup of monkeys (*Ateles vellerosus* Gray) [spider monkey, now *Ateles geoffroyi* Kuhl] was found. He was back in Alvarado on December 22. Early in January of 1826 Deppe paid another, and this time extensive, visit to Valle Real. From there he returned to Alvarado in March and proceeded via Santuario to the city of Vera Cruz which was reached by March 23." In a letter from Deppe to Lichtenstein, translated by Stresemann for A. R. Phillips (in litt.), Deppe states that Valle Real is "on road from Oaxaca [City] to Alvarado, after passing through heavily forested, steep mts. with coyol palm thickets, and still 40 leagues (=10 days in dry season) by pack train from Alvarado."

As noted, the Valle Real shown on the 1840 map is on a "direct route" (trail) between Oaxaca City and Alvarado. Along this route, the only area fitting Deppe's description is in the northeast foothills of the Sierra de Juárez of Oaxaca, a high, "steep"-sloped, "heavily forested" range that borders the flat coastal plain. The trail would certainly have been "very difficult," as is the highway today! Because Valle Real is at the very foot of this range, it could be said to be the place where Deppe "crossed the Cordillera Costal," i.e., he completed the crossing. The forests of the Sierra de Juárez support coyol palm (*Acrocomia mexicana* Karw. ex Mart.; pers. obs.). According to various old Oaxaca maps I have seen, a "league" was equivalent to about 3.8 km. By transferring the trail shown on the 1840 map to a modern map and measuring it, I found the distance from Valle Real to Alvarado to be about 142 km, or 37.4 leagues, close to the 40 leagues mentioned by Deppe.

During his Mexican travels, Deppe collected 958 bird skins, as well as numerous mammals, reptiles, amphibians, fishes, snails, insects, and plants, some of which are still in the Berlin Museum (Stresemann 1954) and probably elsewhere. I have made no attempt to locate his specimens from Valle Real, but the literature refers to those that became types of species or subspecies, as follows (the first locality mentioned is that of the original description): (1) *Aganus braccatus* = *Trogon violaceus braccatus* (Cabanis and Heine 1863), Violaceous Trogon; "Mexico"; syntypes taken in December 1825 and February 1826 at "Valle Real [,Veracruz]" (Stresemann 1954:89; brackets his). (2) *Hylomanes momotula* Lichtenstein 1839, Tody Motmot; "Valle Real, Mexico"; Ridgway (1914:486, in range) lists the locality as "Vera Cruz (. . . Valle Reál . . .)." (3) *Pteroglossus prasinus* = *Aulacorhynchus prasinus* (Gould 1834), Emerald Toucanet; "Mexico"; syntypes taken in December 1825 and in 1828 at, respectively, "Valle Real [,Veracruz] . . . Pico de Orizaba (?)" (Stresemann 1954:89; brackets and question mark his). (4) *Picus castaneus* = *Celeus castaneus* (Wagler 1829), Chestnut-colored Woodpecker; no type locality given; syntypes taken in December 1825 and February 1826 at "Valle Real [,Veracruz]" (Stresemann 1954:89; brackets his). The

A
B
C
D
Villalta
Oaxaca
Zapotitla
Natividad
Papalotitla
Zapotal
Chalcatongo
Ocotitlan
Tuxtepec
Jacatepec
Jotolapa
Tequisistlan
Valle-Flores
Ixcatlan
Yxcatlan
Rio Grande

A.O.U. (1983:397) gives the locality as simply "Veracruz." (5) *Icterus dives* = *Dives dives* (Deppe 1830), Melodious Blackbird; "Mexico"; according to Stresemann (1954:90, 91), the "type," from the "state of Veracruz," was sold, and an extant "cotype" (Berlin Museum) is from "Valle Real [,Veracruz]." The A.O.U. (1983:726) gives merely "Mexico" as the type locality.

In addition, Deppe collected the Black-headed Trogon (*Trogon melanocephalus* Gould 1836 not 1835 or 1838 as usually cited; see Sauer 1982:26–29) at Valle Real in February 1826. This, and a specimen from Alvarado, Veracruz, are listed as types (Berlin Museum) by Stresemann (1954:89), but most other authors (e.g., Miller et al. 1957:12; A.O.U. 1983: 362) consider the state of Tamaulipas as the type locality. Stresemann apparently is in error, because Gould's (1835–1838 [1836]) description clearly gives Tamaulipas, although it is described incorrectly as "a district of Mexico situated between Vera Cruz and the Bay of Honduras." Gould further says that the type "is now in the collection of the Zoological Society of London," not the Berlin Museum.

Published records of non-type specimens from Valle Real are for the Sulphur-rumped Flycatcher (*Myiobius sulphureipygius*) (Salvin and Godman 1888–1904:57) and the Crimson-collared Tanager (*Ramphocelus sanguinolentus*) (Sclater 1856:132). Also, Deppe collected *Dives dives* at "Chiltepec" and "Cosamaloapam," as well as Valle Real (Salvin and Godman 1879–1904:481). There is a San José Chiltepec (not shown, at least by that name, on the 1840 map) 27 km northeast of Valle Nacional toward San Juan Bautista Tuxtepec.

Deppe's collection of the above eight species supports the view that his Valle Real is the same as the one on the 1840 map. *Aulacorhynchus prasinus* is unknown from the Veracruz lowlands southwest of Alvarado but is common in the Sierra de Juárez just above Valle Nacional along the road to Oaxaca City (pers. obs.). The other seven species have been taken more recently at Valle Nacional, where the primary habitat, tropical evergreen forest, is suitable for them (Binford 1989) and for the spider monkey. The December 1825 dates of the Valle Real specimens place him between Oaxaca City and Alvarado, and his presence at San José Chiltepec and Cosamaloapan place him close to Valle Nacional. I know of no other "Valle Real" in Mexico, and no other collector besides Deppe has ever used the name.

In summary, all "Valle Real" specimens and literature records of birds (and other animals and plants) should be referred to Oaxaca, not Veracruz. The type localities should include the originally published locality followed by "=Valle Real [=Valle Nacional], Oaxaca, Mexico."

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FIG. 1. Map, dated 1840, of a portion of Oaxaca and adjacent Veracruz, Mexico, showing the position of (A) "Valle real" [=Valle Nacional] in relation to (B) "Yolos" [=San Pedro Yolox], (C) "Tustepec" [=San Juan Bautista Tuxtepec], (D) "Cosamaluapa" [=Cosamaloapan], and other towns (see text) (map courtesy of the Nettie Lee Benson Collection, The General Libraries, University of Texas at Austin).

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Why female Red-winged Blackbirds call at the nest.—Female Red-winged Blackbirds (*Agelaius phoeniceus*) often give a loud, three or more syllable "chit" call when arriving, sitting on, or departing their nests. These calls, distinguished as "Type I" by Beletsky (1983b), are conspicuous and draw attention to the caller and the location of her nest. Since predation is a major cause of egg and nestling mortality (Young 1964, Caccamise 1976), the calling by females is enigmatic. Beletsky and Orians (1985) tested the hypotheses that female calling signaled the male or signaled to other females, to coordinate group departures. Both hypotheses were rejected, and a third hypothesis, identifying females to their mates to maintain pairbonds, inform the male of reproductive status, and as a consequence, inhibit sexual harassment, was suggested. A subsequent study (Birks and Beletsky 1987) supported this hypothesis by showing that calling inhibited sexual harassment. However, Beletsky and

Orians (1985) established that females called more frequently when departing from a nest site than when arriving at it and that vocalization peaked in the incubation stage and then decreased: both of these patterns are unexplained by the sexual harassment hypothesis. If calling was to avoid harassment, calling should be more frequent at arrival, since the female is more likely to be unmated than one leaving a nest, and calling should peak during prenesting since this is when forced copulations could result in fertilization.

In this study we tested whether females call to signal their identity and nest area ownership by examining when and under what circumstances female Red-wings call, how their vocalizations change over the breeding cycle, and by comparing vocalization frequency between nest aggregations with high and low nest densities in eastern Washington State (EW) and nest aggregations with low nest densities in western Washington State (WW). Two hypotheses were tested: (1) that females call to identify residency and nest area ownership, and (2) that female calls inhibit male harassment.

Female Red-wings vocalize and display during aggressive interactions with each other (Nero 1956b, Beletsky 1983b, Hurly and Robertson 1984), and female aggression may affect settlement of other females (Hurly and Robertson 1985). If calling indicates identity and nest area ownership, we predicted that: (1) females should use the same call when arriving and departing and while sitting on their nests, and (2) calling should be more frequent on densely settled marshes than on marshes with few birds because large numbers of birds arriving and leaving would make visual identification difficult. Further, we predicted that if calling is an aggressive display or to counter male advertisement, calling should occur more often where intrusion by non-resident females is more common and should decrease as female settlement becomes less threatening to a females' fitness.

Study area and methods.—Red-winged Blackbirds were observed at Windmill Lake and Juvenile Lake in the Columbia National Wildlife Refuge (46°56′N, 119°10′W) Grant County, Southeastern Washington on 23, 24, and 30 April and 1 May 1988 for a total of six hours in the early morning and late afternoon. Five groups of birds were studied. Two groups were on isolated territories; each had one male, a preincubating female, and an incubating female. Three groups were part of a large Red-wing nest aggregation with contiguous territories; each of these three groups had one male and four to six preincubating or incubating females. Observations were made from cliffs overlooking the marshes. In WW, we watched birds over the entire breeding season at two ponds near the University of Washington (47°39′N, 122°18′W). From 26 April to 18 May 1988, we observed Red-wings from a 2-m ladder at pond I between 07:00 and 08:00 for a total of 18 h. The pond had two equal sized male territories, and each territory contained two females. A second pond with less vegetation had two territories of unequal size with one female in each. From 9 May to 7 June 1988, observers stood on the shore and watched for a total of 12 h between 07:00 and 08:00. The weather during observations was usually cold and cloudy in both EW and WW. We recorded departures, arrivals, and behavior of all females, the type of call, and the presence and behavior of the male, other females, and predators. The calls were: Type I, three to several "chits"; Type II, a growling "teer" (Beletsky 1983b); and one or two "chets" (Hurly and Robertson 1984). In WW we additionally noted when females called on their nests, whether the call answered the male or another female's vocalization (a call was considered an answer if given within two seconds of an initial vocalization), and if a predator was visible. All chases were noted.

Results.—Most Red-wings in EW nested in densely settled marshes with nest aggregations containing up to about 40 birds; WW birds nested in aggregations as large as six birds. Males in WW held territories more than three times larger than those in marshes in EW. Harem size was between 3 and 12 in EW and between 1 and 4 in WW (Orians 1980, this study). In EW there were more male-male interactions, male aggressive displays, and female-female

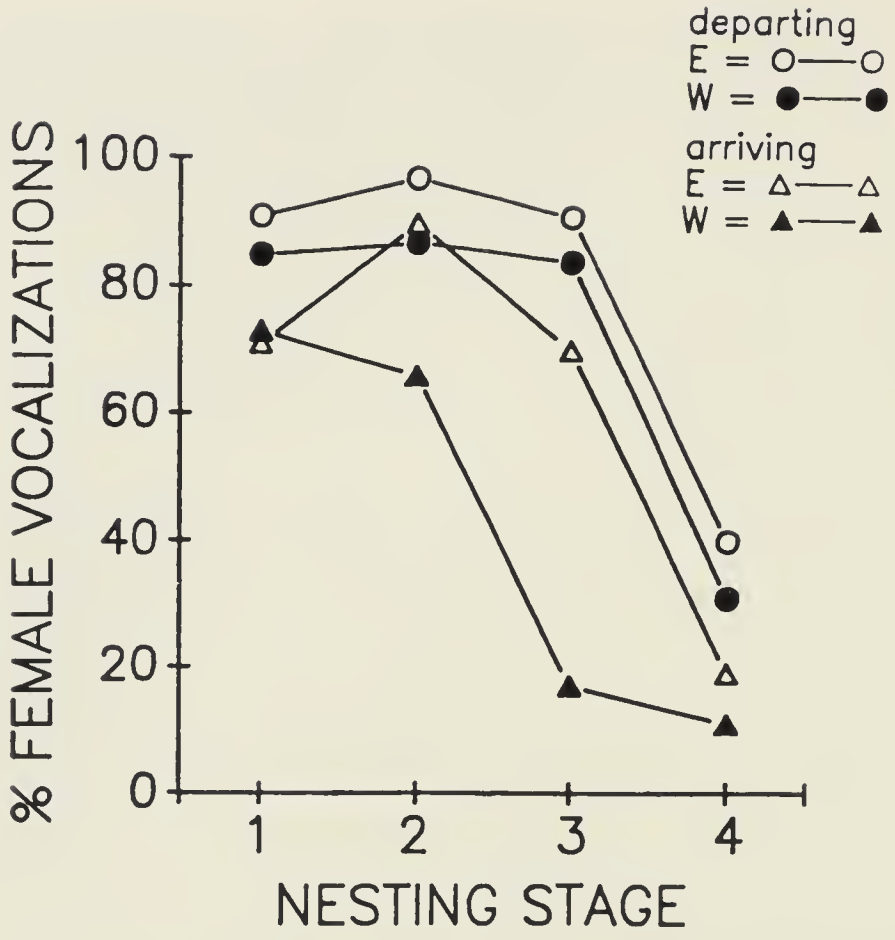

FIG. 1. The percentage of female red-wings vocalizing (Type I) when departing or arriving at their nests. The nesting stages are: 1 = preincubation, 2 = incubation, 3 = nestling and 4 = fledgling. The EW (E) data is from Beletsky and Orians' (1985) study. The WW (W) data is from this study. The pattern of calling for both EW and WW is indicated along with whether the birds were departing or arriving. The number of observed vocal departures over the total observed departures for each stage in this study are: 1 = 18/21, 2 = 96/108, 3 = 100/119, 4 = 13/38. The observed vocal arrivals over the total observed arrivals for each stage in this study are: 1 = 15/20, 2 = 59/91, 3 = 21/118, 4 = 4/46.

and male-female chases than in WW. In WW males fed nestlings and continued feeding fledglings after the females had left the territories.

In both EW and WW, females were most aggressive when other females intruded on their mate's territory. At first, the resident female chased and called (Type I) at the new female when she entered any part of the male's territory. In WW, this distance gradually contracted to about 3 m as the new female built her nest. As intruders became more permanent residents, vocal bouts occurred across what appeared to be a border between their nest areas and lasted up to 15 sec. These interactions often included bill-up displays and wing spreads (see Orians and Christman 1968). Aggressive female activity was observed in both EW and WW and ceased when the intruder laid a clutch of eggs.

All females used Type I calls on and around their nests. In WW 51% of the calls made while females perched on their nests answered their mate's songs ($\bar{x}$ = 51% ± 21%[SD], 8 days, N = 265); in the first minute after his return to the territory 70% of a male's songs were answered (N = 40) and 13% were answered after the first minute (N = 62). Females

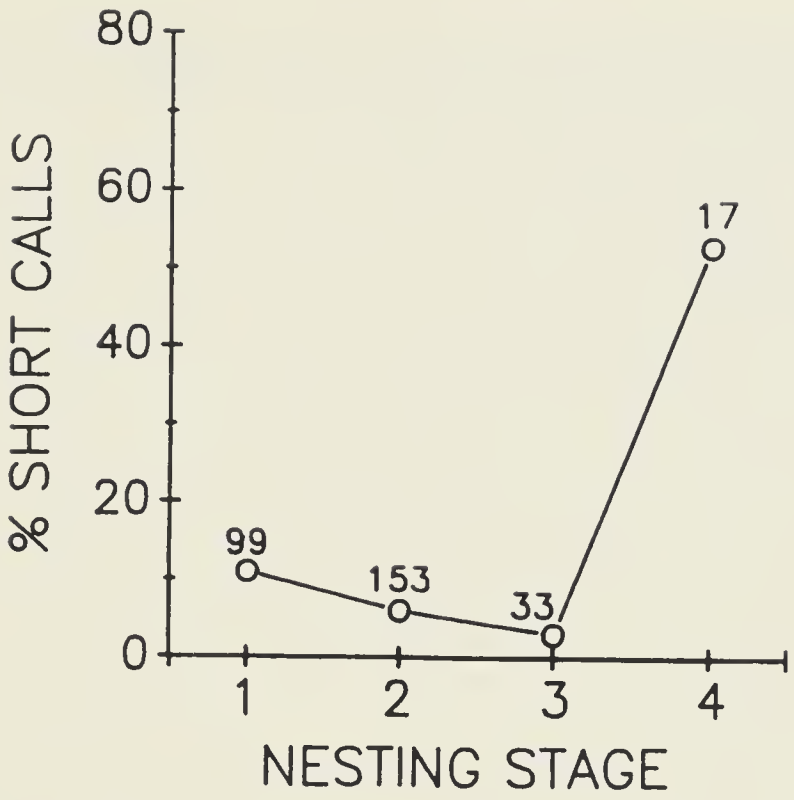

FIG. 2. The percent of short vocalizations, one or two chets, given by red-wing females in relation to nesting stage. Sample sizes indicating the total number of vocalizations given at each stage include both EW and WW data. Stages are: 1 = preincubation, 2 = incubation, 3 = nestling and 4 = fledgling.

were more likely to answer the male in the first minute after his return ($\chi^2 = 35$, df = 1, $P < 0.001$). Eleven percent of the females' calls made from the nest site answered other females' calls (N = 222). These were not correlated with arrivals of other females. During renesting, one female answered only 21% of male and 10% of other females' calls.

Type I and "chet" calls were given during arrivals and departures, but the frequencies changed over the nesting cycle (Figs. 1, 2). Females with nestlings often used Type I calls but occasionally called softly when returning to their nestlings. Females with fledglings rarely called (Fig. 1), and 53% (9/17) of these calls were chets (Fig. 2). Birds did not give Type II calls during observations. The arrival and departure calling of females at both ponds in WW during prenesting and incubation stages was similar and grouped for further analysis ($\chi^2 = 0.3$, df = 1, $P > 0.05$, Fig. 1). The frequency of arrival and departure calling was similar for the different territories in EW ($\chi^2 = 4.9$, df = 2, $P > 0.05$); for preincubating and incubating females these data are similar to the calling rates described in Beletsky and Orians (1985) for both arrivals ($\chi^2 = 0.46$, df = 1, $P > 0.05$) and departures ($\chi^2 = 0.04$, df = 1, $P > 0.05$). Female calling during preincubation and incubation in both our EW and WW sites was also similar for arrivals ($\chi^2 = 0.01$, df = 1, $P > 0.05$), and departures ($\chi^2 = 0.26$, df = 1, $P > 0.05$).

Although the frequency of departure calling in WW was comparable to that described by Beletsky and Orians (1985) ($\chi^2 = 0.06$, df = 3, $P > 0.05$), the percentage of arrivals accompanied by vocalization in WW was significantly lower than they described (Fig. 1), ($\chi^2 = 24.9$, df = 3, $P < 0.001$). Moreover, while Beletsky and Orians (1985) found that the frequency of calling at arrival and departure was similar within each of the four nesting

stages, we found that throughout the breeding cycle calling at departure is more common than calling at arrival in WW ($\chi^2 = 27.8$, df = 3, $P < 0.001$). Finally, in both EW and WW we found that the percent of vocal arrivals and vocal departures decreased over the nesting cycle ($\chi^2 = 246.3$, $\chi^2 = 57.91$, df = 3, $P < 0.001$).

The conditions under which calls were uttered and the consequences of calling varied. When a male was present in WW, females arriving at their nests called more than was expected; females called on 57 of 67 occasions when the male was present and on 12 of 19 when he was absent ($\chi^2 = 6.0$, df = 1, $P < 0.01$). In WW we observed only two short chases by males and both involved silently arriving non-resident females. In EW, the presence of the male apparently did not affect the frequency of calling on arrival; females called on 32 of 45 occasions with the male present and on 31 of 49 when he was absent ($\chi^2 = 0.84$, df = 1, $P > 0.05$). EW males were as likely to chase vocal arriving females (9/32 = 22% chased) as silent arriving females (4/13 = 24% chased), (Binomial Test, $P > 0.17$).

The presence of the male apparently did not affect the frequency of calling during departures in both WW (present: 84% [74/88] vocal vs absent: 77% [14/18] vocal) and EW (present: 89% [49/55] vocal vs absent: 93% [28/30] vocal), ($\chi^2 = 0.5$, $\chi^2 = 0.4$, df = 1, $P > 0.05$). In EW, males were less likely to chase females that called during departures (4/48 = 8% chased) than silent departing females, (3/7 = 43% chased), (Binomial Test, $P < 0.001$). Most male-female chases were short and were never observed to end in copulation. In WW, males were not observed chasing departing females.

Female intrusion was more common in EW where we saw 13 female-female chases in six hours. Only two of these intruding females were silent, suggesting that females were more likely to chase vocal females (Binomial Test, $P > 0.01$, N = 15). We saw females in WW chase females twice during 30 hours; in both cases, intruding females called. All female-female chases were short.

In WW, females' nest areas appeared highly dispersed, maximizing internest distance. When a new female settled, it was at an equal distance between other nests (N = 4).

Discussion.—Calling at all stages is more frequent in EW than WW (Fig. 1). Also, Red-wing densities in EW are greater than in WW. We believe resident females call to identify themselves because the higher activity makes visual identification difficult. By calling, a female quickly communicates her status as a resident before she violates the boundaries of other territories when moving on and off her own territory. Calling inhibited chases by males in EW, supporting the hypothesis that females call to suppress male harassment. Since chasing did not occur in WW, and calling is less frequent, we suspect identification is visual as well as vocal. Since Red-wing nest aggregations are less dense in WW, the advantage of calling for instant identity or ownership status should be lower in WW. Moreover, visual predators such as birds, are relatively less important in EW than in WW; consequently the risk of calling disclosing nests to predatory birds should be higher in WW than in EW. The higher calling frequencies in EW compared to WW is consistent with the idea that benefits of calling in EW are higher than in WW.

Females appear to occupy and defend space within the larger territory of their mates (Nero and Emlen 1951, Hurly and Robertson 1984). Females call to other females when defending their space and in aggressive interactions (Nero 1956a, b, Armstrong 1963, Beletsky 1983b, Hurly and Robertson 1984) and may attempt to prevent other females from settling nearby (Nero 1956a, b, Lenington 1980, Orians 1980, Hurly and Robertson 1985, Searcy 1986). Yet, Searcy (1988) found that female behavior did not appear to affect female settlement. Calling while on her nest, however, may communicate a female's ownership of an area to neighboring birds, and answering another resident's calls may acknowlege their residency. Such calling could help intruding females maximize internest distance and is consistent with the settlement pattern we observed.

The changes in calling frequency we observed over the nesting cycle (Fig. 1) provide insights into why females call. If female calling identifies residency and prevents other females from settling, calling should remain frequent until the female's clutch of eggs has hatched. At this point, the settlement of another female would not affect any male parental involvement in the raising of her young (Yasukawa and Searcy 1981, Beletsky and Orians 1985) as her young will have fledged by the time any new young hatch. Hurly and Robertson (1984) noted a decrease in aggressive and territorial behavior in females in the later part of the nesting cycle. The peak in vocalizations during the incubation stage and the subsequent decrease we observed during the nestling stage is consistent with the hypothesis that females call to both identify their ownership of an area and to discourage other females from settling.

Females also call to communicate with their territorial male (Beletsky 1983b). Female answering from the nest could be both a territorial response indicating ownership and occupancy to the male and a signal to prospecting females that a female is already present. The silent arrivals and departures during the male's absence in WW suggest there is no need to identify oneself and advertise ownership when the male is not present. In EW, however, where density is higher, neighboring males and females must also recognize a female as a resident, so females must call to alert neighbors as well. It is difficult to determine whether male and female chasing is sexual or aggressive behavior. The evidence, however, suggests chasing is territorial. Chasing did not lead to copulation attempts, and calls given by females as they arrived and departed their nests appeared to affect chasing under some circumstances and not under others. In sum, calling does appear to identify resident birds and prevent the harassment that a stranger elicits. Calling may also serve to assert nest area ownership, inhibit intrusion, increase spacing of nests, and delay settlement of other females. The relative importance of calling in each of these functions has yet to be determined. Our results suggest that females call to assert ownership of a nest site and to identify themselves to gain uncontested access to their space.

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Sarcosporidiosis observed more frequently in hybrids of Mallards and American Black Ducks.—American Black Duck (*Anas rubripes*) populations are declining (Kirby 1988). In part, this decline can be traced to the eastward range expansion of the Mallard (*A. platyrhyncos*) (Johnsgard 1961). Additionally, Mallard numbers in the eastern United States have increased through game farm releases (Heusmann 1974). Mallards and Black Ducks hybridize whenever they come into contact (Goodwin 1956, Johnsgard 1967, Heusmann 1974, Ankney et al. 1986), suggesting that these ducks are races of the same species. The lack of behavioral reproductive isolating mechanisms (Johnsgard 1960) is consistent with this interpretation. Black Duck hens, when courted by Black Duck and Mallard drakes, choose Mallards (Brodsky and Weatherhead 1984, Brodsky et al. 1988). Because hybrid drakes tend to exhibit Mallard drake plumage characteristics (e.g., some green on head, white-edged speculum) and because bright plumages among males of *Anas* species presumably evolved through sexual selection (Ankney et al. 1986, Heusmann 1974), it follows that hybrid drakes may be preferred by Black Duck hens over Black Duck drakes. If such preferences exist, then the hybrids pose a special problem for the integrity of the Black Duck phenotype because outcrossing often results in hybrid vigor. Black Duck × Mallard hybrid backcrosses are apparently as fertile as the parental types (Phillips 1915).

Fertility notwithstanding, disease or other factors could reduce hybrid fitness. Here we present retrospective observations that are consistent with this notion. We recorded the occurrence of sarcosporidiosis (a protozoan parasite) in 55 adult (older than 1 year) ducks collected by hunters on three New Jersey state game management areas (Great Bay Management Area, Tuckerton; Dix Management Area, Fairton; Fortescue Management Area, Fortescue) during the hunting seasons of 1986-1988. Juvenile ducks were excluded from

TABLE 1

FREQUENCY OF *SARCOCYSTIS* BY PHENOTYPE IN 56 DUCKS COLLECTED IN NEW JERSEY DURING 1986–1988

Phenotype	Parasitosis	No parasites	Total
Mallard	0	11	11
Hybrid	5	6	11
Black	1	32	33
Total	6	49	55

our sample because advanced sarcosporidiosis is rare among young birds (Cawthorn et al. 1981).

We chose to study *Sarcocystis* for several reasons. First, severe infections are easily identified. Second, the parasite is common in wild duck populations (10% of all individuals; Cornwell 1963). Third, severe sarcosporidiosis could negatively affect fitness (Springer 1984, Box and Duszynski 1978, Tuggle 1987).

Our sample included 33 Black Ducks (17 hens, 16 drakes), 11 Mallards (six hens, five drakes), and 11 drakes that exhibited both Mallard and Black Duck plumage characteristics (i.e., otherwise Black Duck plumage with clearly observable green metallic coloration around and behind the eyes and white-edged speculum). These ducks also had bright yellow bills and orange feet similar to those of Mallard drakes. The 11 drakes with mixed plumage were operationally defined as phenotypic hybrids between the two pure strains (Johnsgard 1968). No clearly identifiable females with mixed plumage characteristics were observed. All ducks were examined for grossly visible *Sarcocystis*, defined as rice-like cysts (2–4 cysts/cm^2) in all surface muscle tissue (i.e., breast, neck, esophagus, and thigh).

The occurrence of *Sarcocystis* by duck phenotype is given in Table 1. There was a significant association between phenotype and parasitosis ($\chi^2 = 16.88$, df = 2, $P < 0.001$) (Conover 1980). To calculate the relative risk of parasitism for hybrids, we compared hybrid phenotype versus the combined frequencies of the pure strains. The relative risk (i.e., odds ratio or cross products ratio) of a hybrid having sarcosporidiosis was 36.27 times that of a non-hybrid. The odds ratio is useful in this context because it is a measure of risk of experiencing an outcome (parasitosis) when an antecedent condition (hybridization) is present (Fleiss 1973).

We speculate that one or more factors could account for our observations. Phenotypic hybrids in our sample may have originated in a location with a high incidence of sarcosporidiosis (relative to those of Mallards and Black Ducks). This explanation seems relatively implausible since the ducks were collected from three widely dispersed areas over the course of three hunting seasons. Another possibility is that phenotypic hybrids may be able to survive parasite loads that kill Mallards or Black Ducks. Finally, and contrary to the notion of hybrid vigor, it is possible that phenotypic hybrids are more susceptible to parasitism. If so, then parasitism may represent a selective pressure against hybridization between the Blaek Duck and Mallard phenotypes.

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Avian removal of fruits from a pokeweed in northwestern Arkansas.—Pokeweed (*Phytolacca americana*), a common herb in disturbed areas of eastern North America, produces bird-disseminated fruits in late summer and fall (Armesto et al. 1983). Flowers are borne on green racemes of varying length and fruits (several mm in diameter) are initially green, becoming pink and finally dark purple when ripe (Armesto et al. 1983, McDonnell et al. 1984). As fruits ripen, racemes also change color to a deep pink, which may aid in fruit removal (Willson and Melampy 1983). Pokeweed fruits ripen asynchronously, a trait associated with temperate plants that fruit in summer (Thompson and Willson 1978, Stapanian 1982, McDonnell et al. 1984). However, pokeweed fruits are typical "low-quality" (Stiles 1980) fall fruits (Johnson et al. 1985).

Waves of migratory fruit-eating birds (primarily catharid thrushes) consume pokeweed fruits in fall in eastern United States as birds move down the Atlantic coast (e.g., Skeate 1987). However, almost no fall migration of frugivorous passerines occurs in the western Ozarks (James and Neal 1986); most fall fruits are eaten by permanent residents, particularly locally produced juvenile American Robins (*Turdus migratorius*) (unpubl. data). Thus, we conducted a study in which ripening and disappearance rates of individual fruits were monitored on a large pokeweed plant from August through October in northwest Arkansas to investigate removal rates of fall pokeweed fruits in the Ozarks in the absence of waves of migratory passerines.

Study area and methods.—Our study focused on fruits on two main stalks of a single large pokeweed plant located along a roadside ditch in a suburban setting one block west of the University of Arkansas, Fayetteville (Washington Co.) campus. This particular plant was chosen because of its size (>3 m tall) and isolation from other pokeweed plants (nearest pokeweed plant = 50 m). We began censusing fruits near mid-day on 18 August 1984, when ripe fruits first appeared and continued mid-day censuses at two-day intervals until 25 October. During each census, numbers of green, pink, purple, and missing fruits were counted on each raceme. Due to alternate branching symmetry of pokeweed plants, each raceme was identified by a unique code, which was written directly on the plant with black indelible ink, based on alternating letters and numbers for branches from the main stalk to the terminal branch, then sequentially numbering racemes on the terminal branch. Numbers of fruits on the ground under the plant also were recorded. A total of 33 censuses were performed; two censuses had to be postponed one day and one census skipped (26 September) due to heavy rains. Casual observations of birds on the pokeweed plant were made throughout the study period.

Results.—A total of 175 racemes was present on the two main stalks, with a mean of 32.3 fruits per raceme (range = 2–67 fruits). Development of green fruits from flowers after censusing began resulted in a peak of 4943 fruits present on 23 August (Fig. 1); only 240 fruits remained when censusing ceased on 25 October. The vast majority of fruits on the plant during August were unripe green fruits, which are not removed by birds (pers. obs.). The number of green fruits present steadily declined as fruits ripened during September and October. Average daily ripening rates generally increased from August through mid-September, meaning that average number of green fruits per raceme generally declined during that period, and ripening rates decreased in late September and most of October (Fig. 2A). (A sharp increase in ripening occurred 1 October following heavy rain and near freezing temperatures the last three days of September.)

Total number of purple fruits present on any given census was relatively low and remarkably constant throughout the study (Fig. 1). Average daily removal rates were highest in late August, but relatively constant through September and early October (Fig. 2B). Few

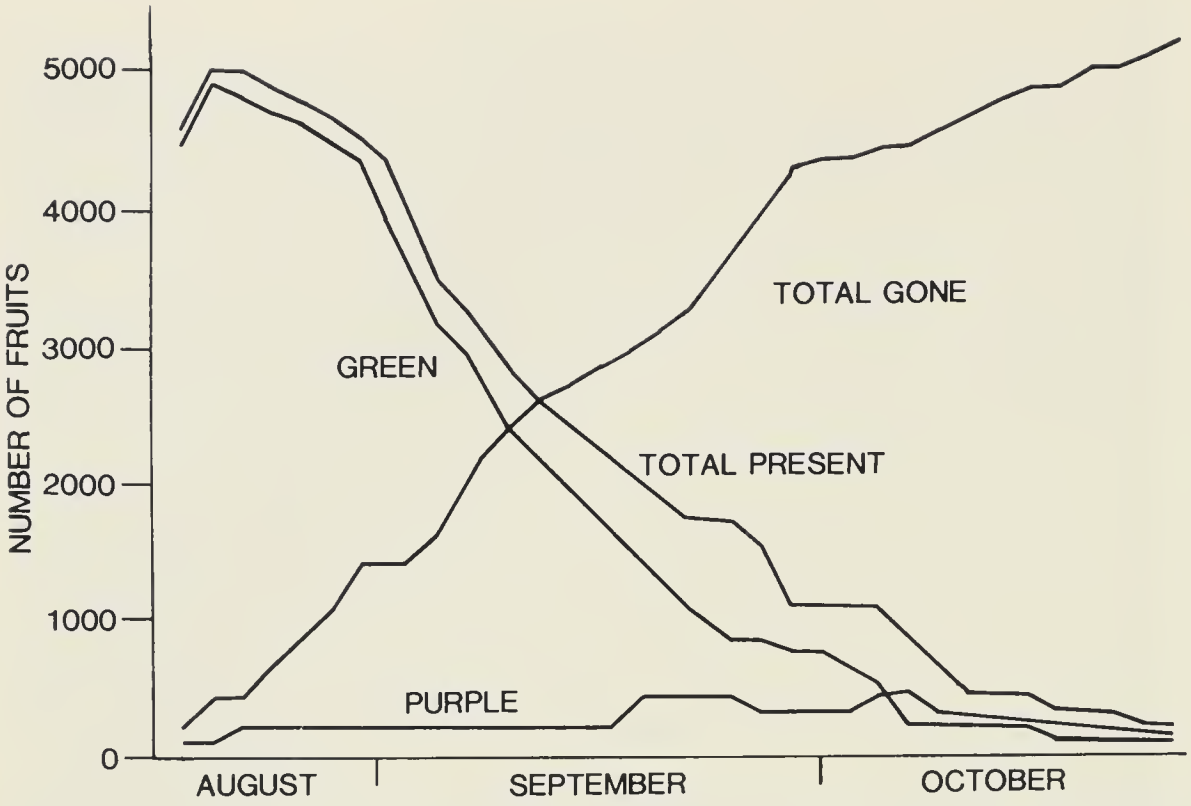

FIG. 1. Number of green, purple, total present, and total missing fruits on the pokeweed plant during the study based on censuses conducted at two-day intervals.

fruits were removed during the late September rain storm, and removal rates were lower in October than during August and September. A significant positive relationship existed between number of fruits removed each day and total number of fruits ($r = 0.56$, $P = 0.001$). The peak number of purple fruits present was 547 on 6 October, which represented 55% of all fruits present that day, and more purple fruits were present than were green fruits throughout most of October. Because of the relatively constant number of ripe fruits, total number of pink and purple fruits removed increased in a linear manner throughout the study (Fig. 1), and a significant negative correlation existed between percent of fruits removed each day and total number of fruits ($r = -0.63$, $P = 0.001$). Ripe fruits were usually missing on from 30–60 racemes between each census.

The only animals observed removing fruits were three species of birds, all of which are permanent residents in northwestern Arkansas. On four occasions, Northern Cardinals (*Cardinalis cardinalis*) were observed eating fruits on the plant, and an American Robin was seen once on the plant. In late August, when removal rates were highest (Fig. 2B), three Northern Mockingbirds (*Mimus polyglottos*) were seen together in early morning on two days removing fruits, and many aggressive interactions were observed among those birds. After that, a single mockingbird (based on characteristic notes in its song) defended the pokeweed plant as a fall feeding territory (e.g., Breitwisch et al. 1986, Logan 1987). That mockingbird often was seen removing fruits during early morning throughout September and October. During the day, it launched aerial attacks against conspecifics and other species of birds from a nearby perch where its view of the plant was unobstructed (see also Logan 1987). We were attacked on two occasions by the mockingbird while we censused fruits. Removal and dispersal of fruits away from the parent plant by birds was very efficient. Nearly 5600 fruits disappeared from the plant during the study, yet we found only six fruits

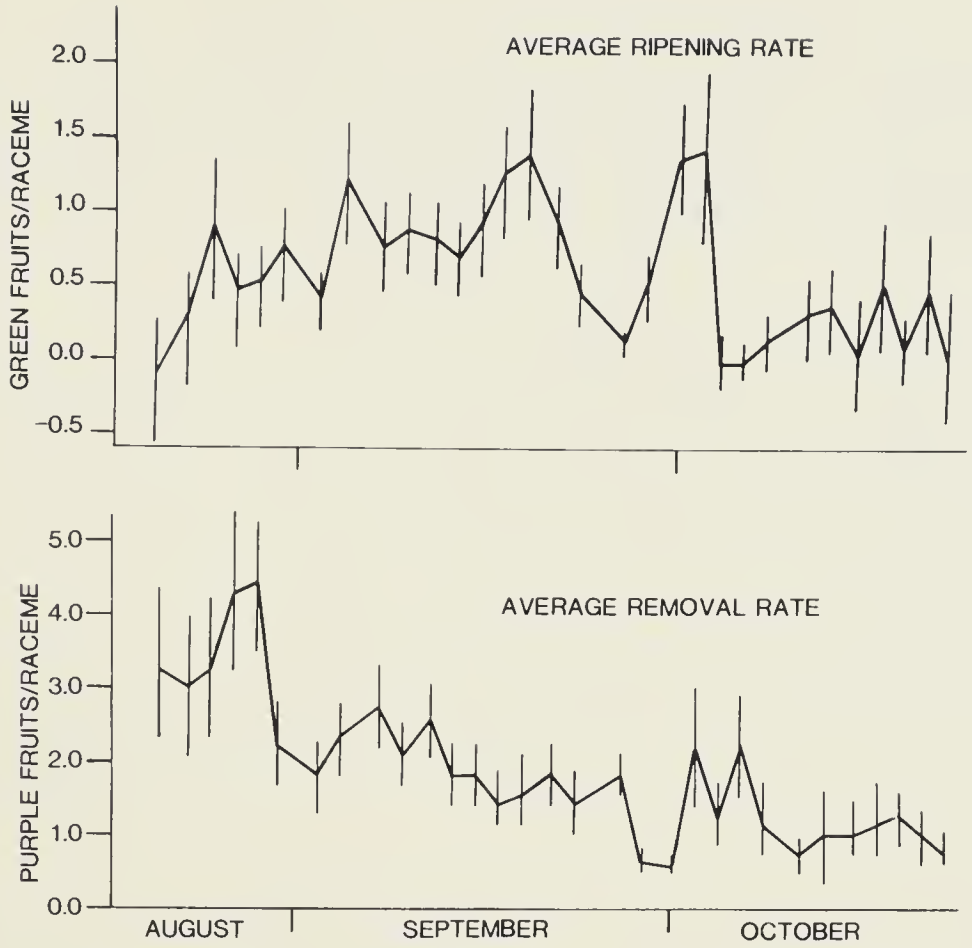

FIG. 2. A. Average daily ripening rate (i.e., average number of green fruits that ripened to pink or purple between censuses) for all racemes that had green fruits on the previous census. B. Average daily removal rate (i.e., average number of purple fruits missing between censuses) for all racemes from which fruits were missing. Bars represent ±2 SE.

on the ground under the plant during censuses. Repeated observations of those six fruits suggest that animals were not removing fruits from the ground between censuses.

Discussion.—Although based on only one large plant, our results suggest that asynchronous ripening of fruits can be a profitable reproductive strategy for seed dispersal during fall at lower latitudes (see Thompson and Willson 1979). Permanent resident birds were attracted to such displays, and nearly all fruits were removed and dispersed over the two-month fruiting period. In addition to the main hypotheses concerning ripening asynchrony as an adaptation for increased reproductive success reviewed by Gorchov (1985), we suggest that an asynchronously ripening fruit crop may attract a territorial frugivore which would ensure an orderly dispersal of fruits.

Avian defense of fruiting plants is uncommon, primarily because fruits usually provide a superabundant food supply that is difficult to defend (e.g., Howe and De Steven 1979, Pratt 1984). Mockingbirds have trouble defending large fruit crops against flocks of frugivores such as American Robins, European Starlings (*Sturnus vulgaris*), and Cedar Waxwings (*Bombycilla cedrorum*) (Moore 1977; K. G. Smith pers. obs). However, mockingbirds (Moore 1977, Logan 1987) and American Robins (Pietz and Pietz 1987) are able to defend fruit crops from individuals and small groups of birds. By removing most ripe fruits on a daily basis, a mockingbird might have greater success at defending an asynchronously ripening

plant such as pokeweed because the majority of the remaining fruits on the plant will be unattractive green fruits that will not attract large numbers of birds.

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"Anting" behavior by Common Grackles and European Starlings.—While anting is not observed frequently in the wild, it appears to be a widespread avian behavior (e.g., Potter 1970, Lilleleht and Maavara 1978, Hendricks 1980, Sanders 1981, Sugihara and Heston 1981, Post and Browne 1982, Simmons 1982, Whyte 1981). Anting has been interpreted as a maintenance behavior in which metabolic products of ants may soothe skin irritated by unusually rapid feather replacement (Potter 1970, Potter and Hauser 1974). Anting may also function to control ectoparasites and pathogens found on the skin and feathers by supplementing the natural properties of preen waxes, which are known for their antibacterial and antimycotic properties (Pugh 1972, Pugh and Evans 1970, Ehrlich et al. 1986). The latter explanation is plausible because *B*-hydroxy fatty acids found in ants are strongly fungicidal (Schildknecht and Koob 1971, Beattie 1985), and coincidentally, these fatty acids are also a major uropygial secretion of several species of birds (see Jacob and Ziswiler 1982). If birds are using the intrinsic "soothing," antimicrobial, or possibly the antiarthropod, properties of ants, we hypothesize that birds should recognize these properties in other organisms or objects which might yield the same end result. Indeed, birds have been seen "anting" with millepedes as well as with marigolds (*Calendula officinalis*) (Clunie 1976, Eyles 1983, Dennis 1985). Millepedes have powerful defensive secretions used against arthropods (Monroe et al. 1962.). Marigolds reportedly have antibacterial properties, and the petals contain sitosterol (Duke 1987), a chemical known to inhibit oviposition in Acarid ticks and mites (Ambasta 1980). Consistent with the above hypothesis, we report "anting" by Common Grackles (*Quiscalus quiscula*) and European Starlings (*Sturnus vulgaris*) using mothballs. Commercially available mothballs are composed of naphthalene, a chemical known for its insecticidal and repellent properties.

Early in the spring of 1988, we placed mothballs in a flowerbed which bordered a vegetable garden in the suburbs of York, Pennsylvania. The garden was located 12 m from a sunroom. Overall, the weather for the observation period was sunny, with mean maximum and minimum temperatures and relative humidities of 29.5°, 15.5°C and 79%, 31.4%, respectively. On the afternoon of 24 June 1988, we saw a Common Grackle attempt to pick up a mothball. After several attempts the grackle succeeded in holding the mothball in its beak. It then extended its left wing and rubbed the mothball up and down the length of the shaft of each secondary feather. Subsequently, the grackle rubbed the mothball throughout the secondary coverts on the ventral side and into the propetagium area. The grackle then repeated the same rubbing pattern on its right wing. The entire rubbing pattern lasted 10 min, after which the grackle dropped the mothball and flew away. On subsequent days (26 and 28 June), we observed a grackle pick up a mothball from the garden and fly to a perch. At these times the garden was in full afternoon sun, while the perches were shaded. In both instances, the rubbing pattern followed that described above. After both wings were rubbed with the mothball, the grackle would drop the mothball. These observations would explain our earlier and frequent observations of finding mothballs in areas of the yard quite different from their original placement.

The observation that grackles use mothballs in "anting" behavior has been reported previously (Dubois 1969). But grackles are not the only species for which this behavior has been observed. In discussing this behavior with Mrs. Naadi Perry of Washington, D.C. (pers. comm.), we learned of similar behavior by European Starlings. On at least four occasions in June 1985, starlings were seen picking up mothballs from a garden and rubbing their wing feathers in a manner similar to that described for grackles.

How do birds recognize objects to employ in "anting" types of behavior? The classes of objects or organisms reported in the literature invariably have antimicrobial or insecticidal

properties. There are no reports that birds exhibit "anting" with objects or organisms that are unlikely to possess such properties. If birds are selecting objects based on their chemical properties, then they must be able to discriminate such objects using chemical cues. It generally is believed that passerines have a poorly developed sense of smell (Bang and Cobb 1968). However, recent studies have shown that at least two passerines, starlings and Brown-headed Cowbirds (*Molothrus ater*) have an olfactory sensitivity comparable to birds with more well developed olfactory anatomies (Clark and Mason 1989, Clark and Smeraski 1990). Also, it may not be unreasonable to suggest that birds can make the associations necessary for anting. Clark and Mason (1985, 1987, 1988) have shown that starlings use the chemical attributes of plants to decrease parasite and pathogen load at nests and that they may use olfaction as a means to discriminate among plants. We suggest that future studies focusing on anting consider the behavioral capabilities of birds to perceive chemical cues of high biological relevance.

In the context of our current observations, it should be noted that naphthalene is registered by the U.S. Environmental Protection Agency as a bird repellent. Clearly, the seven observations indicate that at least two or more birds were not repelled by naphthalene, suggesting that the types of compounds that are repellent to arthropods may not be repellent to birds (e.g., Dolbeer et al. 1988).

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Nest predation of Plumbeous Ibis by Capuchin Monkeys and Greater Black Hawk.—The Plumbeous Ibis or "Curicaca" (*Harpiprion caerulescens*) is a neotropical species patchily distributed from Tucumán in Argentina north to Mato Grosso in Brazil, Paraguay and Central Bolivia (Meyer de Schauensee 1970). It is uncommon and little known, but information on its general ecology and behavior is available (Belton 1984, Sick 1985, Cintra 1986). In the Pantanal region of Mato Grosso, along the Transpantaneira Highway (about 56°55′W, 17°16′S), I have found this species to be fairly common and I located some nests which contained from eggs to young near fledging (up to three per nest) in August–September. This may indicate two consecutive clutches per year. Unlike other ibises, the Curicacas do not nest in colonies, nests being constructed more commonly on the horizontal limbs of huge fig trees (4 of the 5 nests), I found from 8 to 20 m high. The nest is made of twigs, resembling that of the Wood Stork (*Mycteria americana*).

In the early morning of 5 September 1987, while I followed a group of three capuchin monkeys (*Cebus apella*) in a forested area near the Transpantaneira Highway, one of the monkeys located an ibis' nest about 15 m high on a leafless tree. The monkey climbed to the nest, and immediately was faced by the brooding ibis. The sitting bird threatened the monkey with its half-open bill and uttered harsh cries, trying to strike as the monkey came closer. At each of the bird's attacks the monkey hit it on the head with one hand, managing

to approach and grasp one egg from under the bird as it retreated after such a blow. While the ibis and this monkey engaged in this fighting, a second monkey approached from behind the bird and took an egg from within the nest, almost at the same time the first monkey succeeded in stealing the other egg. Both monkeys moved to lower branches and sucked the eggs, dropping the empty shells and moving away. The bird kept on the nest all the time the monkeys were nearby, screaming.

On 1 September 1988, I found an ibis sitting in a nest, about 20 m high on a limb of a fig tree by a swamp. The following day, at about 16:00 p.m. the screaming of the bird called my attention, and I found an immature Greater Black Hawk (*Buteogallus urubitinga*) on the ibis' nest. One parent ibis was screaming on a branch immediately below, the anterior portion of its body and wings lowered, its bill half-open and pointing at the hawk, its neck, body and tail feathers bristled. The hawk picked up one of the eggs with its bill and dropped it in the nest. The ibis flew to the nest, landed on the edge, and tried to strike the hawk with its bill. The hawk defended itself with one of its talons, and with two strikes made the ibis withdraw to a lower limb. The hawk clumsily picked up the two eggs one at a time dropping them several times and eventually managed to break the shells and ingest the contents. In the meantime, the ibis hopped from one branch to another, screaming and grooming itself.

The defensive behavior of the Plumbeous Ibis at its nest does not seem to be effective against large and agressive nest-robbers such as monkeys and large hawks but could deter smaller or weaker predators such as opossums, jays, and vultures. This agressive behavior may also serve to discourage a less motivated predator. Plumbeous Ibises protest strongly against human beings near the nest by screaming, flying only when people are too close. This contrasts with the behavior of the colonial White Ibis (*Eudocimus albus*) that may depart readily from humans and seems more timid toward predators (Bent 1926).

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Predatory behavior of captive Greater Roadrunners feeding on horned lizards.—Little information is available concerning Greater Roadrunner (*Geococcyx californianus*) predation on horned lizards (*Phrynosoma*) (Bryant 1916, Milne and Milne 1950), broad-bodied lizards with ossified spiny horns. Sutton (1913, 1915, 1922, 1940) identified "horny frogs" (*P. cornutum*) as prey, noting that small ones were swallowed live and older ones are beaten before being swallowed. Roadrunners attempting to prey on juvenile and adult *Phrynosoma* of the seven species inhabiting the southwestern United States (Sherbrooke 1981), which differ in size and anti-predator morphology and behavior, encounter varied problems dispatching and swallowing these lizards. These variations in lizard defensive ability may influence selection of prey by the birds.

Here I document the ability of roadrunners to prey on adults of both a large, well-armored species, the Texas horned lizard (*Phrynosoma cornutum*), and on a small, relatively defenseless species, the round-tailed horned lizard (*Phrynosoma modestum*). Attack and ingestion behaviors of roadrunners are described, as are the anti-predator behaviors of the two *Phrynosoma* species.

Methods.—Two nestling roadrunners were captured in the San Simon Valley, Cochise County, Arizona on 1 June 1988 under Federal Fish and Wildlife Permit No. PRT-715774 and Arizona Game and Fish Dept. Permit No. 0001. Both were hand-reared. The development of predatory skills was encouraged by releasing the birds for foraging bouts outside the cage and by a sequential presentation of dead, live chilled, and later, fully active lizards. Birds were fed twice daily. They were fasted overnight before trials. Weights of roadrunners #1 and #2 on 6 August 1988 were 366 and 315 g, respectively.

Ten predator-prey trials with adult *P. cornutum* and 12 trials with adult *P. modestum* were conducted with two roadrunners from 30 July–12 August 1988. Predator-prey trials were conducted between 09:20 and 11:45 MST at air temperatures between 24.9° and 32.3°C, usually in full sun. Trials were held in an outdoor 5.5 × 4.6 × 2.2-m aviary at the Southwestern Research Station of The American Museum of Natural History, Portal, Arizona. All *Phrynosoma* were adults collected during May, June, and July 1988 from Hidalgo County, New Mexico, and Cochise County, Arizona, under Arizona Game and Fish Dept. Permit No. 0001 and New Mexico Dept. Game and Fish Permit No. 1149. In captivity they were fed ants.

A blind was not used since roadrunners and horned lizards were habituated to the observer. In each trial, one lizard was placed on the ground in front of one of the roadrunners. Trials (N = 13) of Roadrunner #1 always preceded trials (N = 9) of Roadrunner #2. Trial numbers are sequential for each bird. Notes and photographs were taken of roadrunner behaviors associated with killing and swallowing lizards and of *Phrynosoma* defensive behaviors. If roadrunners showed little interest in the lizard (rejected) the trial was terminated after 15 min, including 7 and 13 min in two cases in which the bird deserted the lizard. If a roadrunner rejected a *P. cornutum* (this species was always offered first), a *P. modestum* subsequently was presented (two or three trials of this species in sequence), thus verifying the bird's interest in feeding and providing trials of predator-prey interactions with this species.

Trial results.—In five of the ten trials with *P. cornutum* the lizards were killed and eaten (50%); in the other five trials the lizards were rejected (50%). In 11 out of 12 trials with *P. modestum* the lizards were eaten (92%); only one lizard (8%) was rejected by a roadrunner that had just eaten two *P. modestum*. The duration of five fatal trials involving *P. cornutum* was significantly longer ($\bar{x}$ = 22.5 min) than the duration of 11 fatal trials with *P. modestum* ($\bar{x}$ = 1.6 min; t = 4.804 with 14 df and $P_{.01}$ = 2.977).

Roadrunner #1 ate the first two *P. cornutum* offered during trials and then rejected the

following three *P. cornutum.* The last *P. cornutum* eaten was swallowed with difficulty (see below). Roadrunner #2 killed and ate one *P. cornutum,* rejected a second, and ate two more during subsequent trials before rejecting a fifth.

In four trials, *P. cornutum* attempted running escapes at the beginning of the trial. These movements elicited rapid chase by the roadrunner. In response to being attacked or overtaken, lizards: (1) arched their body upwards (similar to the "rain-harvesting" stance; Sherbrooke 1988) and rocked forwards and backwards on their legs, while facing the roadrunner, or (2) lifted their side farthest from and lowered the side nearest to the roadrunner, while dorso-ventrally flattening and laterally extending their abdomen, thus presenting a large surface ("dorsal-shield"; Sherbrooke 1988) which was repeatedly oriented toward the bird by repositioning. If approached, the lizard thrust its head in the direction of the roadrunner ("horn-threat"; Sherbrooke 1988). After being bitten or pecked several times, the lizard almost always inflated its body, thus increasing in size, erecting dorsal spines on the abdomen, and extending lateral fringe scales. The air-inflated body may also provide a degree of "shockproofing," causing the lizard to bounce during battering "centrifugal-slams" (see below). In a few trials, after extended roadrunner attack, the lizard assumed a "head tilted back posture" (Sherbrooke 1987, 1988), but in no case was a "horn-raised response" (Sherbrooke 1987, 1988) noted. In two trials, lizards briefly engorged their circumorbital sinuses with blood, but "defensive" blood-squirting (Sherbrooke 1981, 1988, Sherbrooke and Montanucci 1988), seen in encounters with some predatory mammals (Sherbrooke pers. obs.), never occurred. Attacking roadrunners grab a lizard by the head or body and smash it against the ground (in only a few cases were rocks used as battering surfaces). Repeated pecking and biting failed to penetrate the lizard's tough, elastic skin which contains an abundance of collagen fibers (Sherbrooke 1988). Horned lizards are ingested whole. Roadrunners made no efforts to break the lizard's potentially lethal horns (see Sherbrooke 1981, 1987, 1988, Sherbrooke and Montanucci 1988, and references therein). Horns were not broken during battering of the lizard in any trial.

In all trials, birds repeatedly utilized a previously unreported, "centrifugal-slam" technique to stun or kill the lizards. For the centrifugal-slam, the bird grasps any leg or the tail in its beak, rapidly raises its head and neck (tilting its head to one side) and swings the outwardly forced body of the lizard upwards and around through a vertically extended, oval-shaped trajectory which culminates in a downward accelerating slam against the ground. During the swinging, the bird's body remains stationary. Photographs at 1/250 and 1/500 sec show that the nictitating membrane covers the eye during the procedure. In one trial, repeated centrifugal-slams were counted over 5 min. The frequency was 20.8/min.

Roadrunners begin ingestion of the lizard by grasping its head in their bill and rapidly thrusting, repeatedly, their open jaws forward to surround the head and forebody. In most cases, the body of the lizard was greatly inflated during swallowing. All *P. cornutum* were swallowed head first, and usually were completely inverted, so that the dorsal head horns were aimed down and were, therefore, less threatening to the bird's vital organs if they happened to puncture the esophagus. Once the lizard passed beyond the bill, the birds maintained their necks upright and extended. In two trials, the roadrunner folded its upper neck to the side, at a 90° angle to the upright position, in an apparent effort to push the large prey farther down its esophagus. No pellets were regurgitated, and digestion of all parts was apparently complete.

Of the experimental *P. cornutum* of known size, the four eaten were not significantly smaller in snout-vent length (SVL $\bar{x}$ = 86.2 mm) than the four rejected (SVL $\bar{x}$ = 91.7 mm; t = 1.558 with 6 df and $P_{.05}$ = 2.447). The one unmeasured adult *P. cornutum* used on 10 August was rejected by Roadrunner #1 and eaten by Roadrunner #2.

In two trials, half-ingested lizards were regurgitated repeatedly (five times, Roadrunner #1, trial 2; three times, Roadrunner #2, trial 1), re-battered each time, and finally swallowed. In both trials, the saliva-covered heads of the lizards showed traces of blood, possibly due to punctures or abrasions of the birds' esophagus. Roadrunner #1 refused all *P. cornutum* offered after trial 2. Roadrunner #2 refused a *P. cornutum* after a similar experience (trial 1) but later ate two *P. cornutum* before rejecting a third.

Several *P. modestum* initially attempted running escapes. In a few trials, the roadrunner located a motionless lizard by circling the prey in a narrowing spiral. When captured, lizards exhibited dorsal-shield displays if given the opportunity, but ingestion occurred so rapidly in many trials that the lizard had little time for defensive behaviors. Only two inflated their bodies. None utilized the horns-raised or head-tilted-back responses, horn-threat, or defensive blood-squirting. In half the trials, *P. modestum* displayed mouth-open threats at the roadrunner. These were not seen in *P. cornutum* trials. Mouth-open threats were noted by Sherbrooke (1988) in both species when confronted by predatory grasshopper mice (*Onychomys torridus*).

Most commonly, the roadrunners held *P. modestum* by the body in their beak and battered them against the ground. The centrifugal-slam technique was used much less frequently than with *P. cornutum*. Lizards were ingested head first, often dorsal side up, and usually while still alive. Few problems were encountered with swallowing these smaller lizards. Roadrunner #1 bled from a wound that occurred when a horn penetrated the tissues on the inner surface of the tip of its upper mandible. Bleeding occurred on two successive days (trials 5 and 8); it did not inhibit predation. The only *P. modestum* rejected, Roadrunner #1 (trial 13), was subsequently eaten the same day, Roadrunner #2 (trial 9). This animal was unmeasured. The average snout-vent length of ten *P. modestum* in fatal trials was $\bar{x}$ = 52.3 mm.

Discussion.—Predation by captive roadrunners was lower on adult *P. cornutum* (50%) than on adult *P. modestum* (92%). The former (SVL $\bar{x}$ = 86.2 mm) were significantly larger than the latter (SVL $\bar{x}$ = 52.3 mm; t = 7.828 with 12 df and $P_{.01}$ = 3.055). Roadrunners may have learned to avoid large, well-armored adult *P. cornutum* following difficulties in swallowing. Sherbrooke (1988) reported a similar size-related difference in mortality of the same two horned lizard species when attacked by captive southern grasshopper mice (*O. torridus*). Munger (1986), working with wild populations, found the rate of death due to predation to be higher in *P. modestum* than in *P. cornutum*. In the wild, roadrunners may refrain from attacking adult *P. cornutum* if other foods are available. Sutton (1940) states that horned "frogs" are not eaten unless other food is difficult to obtain. Roadrunners appear to have several prey specific handling behaviors, i.e., plucking feathers from avian prey (Sutton 1940, Zimmerman 1970) and seizing scorpions by the tail (Sutton 1913). The centrifugal-slam technique may be specifically employed on large-bodied prey, such as *P. cornutum*.

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Aggressive interactions in wintering House Finches and Purple Finches.—As a result of its introduction in 1940 and subsequent population expansion, the House Finch (*Carpodacus mexicanus*) is now widely sympatric in the eastern United States with the Purple Finch (*C. purpureus*) (Elliot and Arbib 1953, Bock and Lepthien 1976, Aldrich and Weske 1978). It seems possible that two such similar and closely related species may interact with each other in significant ways, particularly during the winter when both species are frequently foraging at bird feeders. This study reports the results of encounters between House and Purple finches at a bird feeder in Lynchburg, Virginia.

Methods.—From 23 December 1985 through 31 March 1986, dyad interactions resulting in displacement of the losing individual were recorded at a backyard bird feeder. A total of 1585 displacement interactions involving House Finches and Purple Finches in intra- or interspecific encounters were seen during 1065 minutes of observation (71 recording periods, each 15 min long). The feeder used was rectangular (22 × 30 cm) with a narrow (6 cm) shelf on each side that accommodated a total of approximately 10 birds. Food offered consisted exclusively of "oil" sunflower seed. Competition for space on the feeder was intense and the turnover of feeding individuals due to displacement was frequent. The loser of a displacement encounter was forced to relocate on the feeder, or more frequently, to leave the feeder. The winner and loser of each encounter was placed in one of four categories. Because adult female House Finches and adult female Purple Finches are difficult to distinguish from yearlings of both sexes (Bent 1968), these categories were: (1) male House Finch, (2) female-plumaged House Finch, (3) male Purple Finch, or (4) female-plumaged Purple Finch.

TABLE 1
FREQUENCIES OF MALE AND FEMALE-PLUMAGED HOUSE FINCHES AND PURPLE FINCHES ATTEMPTING TO USE FEEDER

Spp./sex	Total obs.	% Obs.	Mean/period	SD
House				
Male	781	21.8	11.0	3.11
Female	1235	34.5	17.4	3.44
Purple				
Male	454	12.7	6.4	2.27
Female	1108	31.0	15.6	3.17
	3578[a]			

[a] 3578 birds/71 periods = 50.4 birds/period, SD = 5.25.

The total number, as well as the relative frequency, of birds in a category are variables that potentially may affect the success of a bird in that category in a displacement interaction. The data for this study, however, were compiled from recording periods in which the numbers of birds in each category were fairly constant, both within each recording period and over the entire course of the study (Table 1).

The results of displacement interactions were analyzed for significance using chi-square tests.

Results.—About 38.6% of the observed interactions were between House Finches, 33.4% were between Purple Finches, and 28.0% were interspecific encounters. These observed frequencies differ significantly from the frequencies that could have been expected if birds of each species interacted in proportion to their frequency in the population attempting to use the feeder ($\chi^2 = 333.74$, df = 2, $P < 0.05$). Since interspecific interactions were 21.2% lower than expected, it appears that birds preferentially sought out members of their own species when making a displacement attack.

When interspecific interactions occurred, House Finches were likely to win at a rate greatly exceeding their frequency of occurrence in the population attempting to use the feeder (90.9% = 404/444 observations). Although Purple Finches made up 43.7% of the total birds competing for a place at the feeder, they were able to win only 9.0% of the interspecific displacement interactions, significantly less than expected ($\chi^2 = 217.1$, df = 1, $P < 0.05$).

In House Finches the frequency of intraspecific displacement interactions based on plumage type (male vs female-plumaged) did not differ significantly from the population frequencies for each plumage type (Table 2, $\chi^2 = 3.1$, df = 2, $P < 0.05$). The same was true for Purple Finches (Table 2, $\chi^2 = 0.8$, df = 2, $P < 0.05$).

In House Finches female-plumaged birds won intraspecific displacement interactions with males more frequently than would have been expected based on their frequency in the general population of House Finches (71.3% = 219/307 observations, vs 61.3% expected, $\chi^2 = 13.2$, df = 1, $P < 0.05$). The same was true to an even greater extent in Purple Finches (95.6% = 216/226 observations, vs 70.9% expected, $\chi^2 = 67.1$, df = 1, $P < 0.05$).

During interspecific displacement interactions, male and female-plumaged House Finches were about equally successful at displacing Purple Finches (males, 91.2% = 177/194 observations; females 90.8% = 227/250 observations). This was true even though male House Finches were outnumbered by female-plumaged Purple Finches.

TABLE 2

FREQUENCIES OF OBSERVED DISPLACEMENT INTERACTIONS COMPARED WITH EXPECTED DISPLACEMENT INTERACTIONS FOR ALL INTRASPECIFIC DYADS

Spp./sex	Obs. no.	% Obs.	Exp. no.	% Exp.
House Finch				
Male-male	96	15.7	92	15.0
Female-female	209	34.1	230	37.6
Male-female	307	50.2	290	47.5[a]
Total	612		612	
Purple Finch				
Male-male	47	8.9	45	8.5
Female-female	256	48.4	266	50.3
Male-female	226	42.7	218	41.3[b]
Total	529		529	

[a] $\chi^2 = 3.1 < 6.0$, 2 df, $P < 0.05$.
[b] $\chi^2 = 0.8 < 6.0$, 2 df, $P < 0.05$.

Discussion.—House Finches may be competitively superior to Purple Finches when foraging at bird feeders. Both male and female-plumaged House Finches won the great majority of their displacement interactions with Purple Finches. Also, although space at the feeder was very limited and competition for feeding places was strong, interspecific interactions were 21% lower than expected. The lower than expected percentage of interspecific interactions can mainly be accounted for by an unexpectedly high level of intraspecific Purple Finch interactions. Purple Finches may have been avoiding aggressive interactions with House Finches, choosing to attempt to displace members of their own species instead.

The intraspecific dominance displayed by female-plumaged House Finches in this study was also reported for House Finches by Brown and Brown (1988). Male House Finches, however, were as successful as female-plumaged birds at dominating Purple Finches. Also, preliminary analysis of data on House Finch displacement interactions with American Goldfinches (*Carduelis tristis*) indicate that male House Finches were actually somewhat more successful in dominating this species than were female-plumaged birds (males winning 61% displacement interactions to 48% for female-plumaged birds). Both of these results suggest that male House Finches were at least as aggressive as female-plumaged House Finches and, thus, may have actually been deferring to female-plumaged birds, rather than being defeated by them. Brown and Brown (1988) found similar evidence of male House Finches deferring to female-plumaged birds.

Since this behavior was even more pronounced in Purple Finches (males losing/deferring 95.6% of the time versus 71.3% in male House Finches), it may be typical of *Carpodacus* finches in general. The higher rate at which male Purple Finches lost/deferred to female-plumaged birds may have been the result of interspecific differences in the "female" plumage of yearling male Purple Finches and yearling male House Finches. Yearling male Purple Finches are indistinguishable from adult females (Bent 1968); yearling male House Finches, on the other hand, sometimes show traces of red (Michener and Michener 1931). Consequently, male Purple Finches may have more difficulty than male House Finches in distin-

guishing yearling males from adult females, leading them to lose/defer to a greater number of female-plumaged birds.

Brown and Brown (1988) cite Rohwer (1986), noting that if males defer to females during displacement encounters, it would be to the advantage of yearling males to have a plumage type similar to that of the females, thus gaining a competitive advantage during competition with males for resources. While Smith (1980) pointed out that females of many species are dominant to males during the breeding season, there is no apparent reason why males should defer to females during the winter (Brown and Brown 1988).

Brown and Brown (1988) suggest the possibility that male House Finches may remain paired with their breeding partners during the winter and defer to their mates at all times of the year. Males in the present study, however, deferred to many females, so this explanation seems unlikely. A more tenable hypothesis stems from the considerable variability in plumage that is typical of male House Finches, some of which is age-based (Michener and Michener 1931). If female House Finches learn to recognize individual males based on their plumage type and then avoid mating with males that have treated them aggressively during the winter, males would be subject to strong pressure to defer to females. Perhaps a male's willingness to defer to a female during the winter might also provide an indication of his willingness to defer during the breeding season.

Whether the increasing numbers of House Finches in Virginia will have any long term impact on the wintering numbers of Purple Finches in the state remains to be demonstrated. House Finches have become very abundant in Virginia. The species was first recorded in the state in 1962 (Murray 1963), and the first Christmas Bird Count record was made in 1966 (Scott 1967). House Finches have been breeding in Virginia since at least 1976 (Blem and Mehner 1979), and their numbers have increased greatly since then (Root 1988).

It is not possible at this point to show that the introduction of the House Finch into the eastern United States is causing a reduction in Purple Finch populations. It is possible, however, that the expanding House Finch population could have a negative impact on Purple Finch numbers, especially during particularly stressfull winters, when both species frequently forage at bird feeders. This may be particularly true, because as the relative frequency of House Finches increases at a feeder, Purple Finches may simply lose out by default, as they avoid interacting with the more numerous, and apparently more aggressive, House Finches.

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Nest-site selection of the Common Wheatear in high mountain areas of southeastern Spain.—The nest site and its surrounding microhabitat are two fundamental elements that act both as proximate factors in territorial establishment (Hildén 1965) and as ultimate factors conditioning reproductive success (Wray and Whitmore 1979). Despite the fact that the microhabitat may be as important to the bird as the nest site itself (Martin and Roper 1988), few works have concentrated on the characteristics of the microhabitat surrounding the nest (but see Mackenzie and Sealy 1981; Clark et al. 1983; Petersen and Best 1985a, b). This note describes the nest site and the immediate microhabitat surrounding the nests of the Common Wheatear (*Oenanthe oenanthe*).

Common Wheatear nests were found during a random survey carried out between 2000 and 2800 m a.s.l. in the pasture-scrubland of the high-mountain area of the Sierra Nevada in southeastern Spain (see Zamora 1988 for a detailed description of the habitat). Sampling of the nest microhabitat and the territorial habitat was carried out in the following manner: four lines, each 15 m long, were traced outwards from the nest, the first direction being chosen at random and the other three following successively at 90° angles. The first sample within each line was taken at 25 cm from the edge of the rock covering the nest and the next three at further 25-cm intervals up to 100 cm from the rock. In this way 16 samples were obtained of the microhabitat immediately surrounding the nest. Five more samples spaced at 3-m intervals were taken along the remaining 14 m of each line, giving a total of 20 samples of the sector of territory surrounding the nest. The data were obtained by sticking a round metal rod, 1 cm in diameter, vertically into the ground at each sample point and noting the type of substrate that touched the bottom of the rod and at 5-cm intervals throughout its height (as described by Wiens and Rotenberry 1981). The following variables resulted (the corresponding nomenclature used in Table 1 appears in brackets): (1) The main elements covering the habitat (in percent cover): herbaceous layer (GRASS); total shrub cover (SH.CO), including *Genista baetica* (GENI) and *Juniperus communis* (JUNI); bare ground (BARE); litter (LITTER); and rocks (ROCK). (2) Vegetation structure: HIT.$\bar{X}$ = average number of hits per sample; MAX.H = the height of the highest shrub encountered along all four sample lines; DIV.I = diversity index of the vertical profile of the shrub layer; and HET.I = horizontal heterogeneity index of the vegetation (Wiens 1974).

TABLE 1

THE MEANS AND STANDARD DEVIATIONS OF THE REPRESENTATIVE VARIABLES FOR THE TERRITORIAL AND NESTING MICROHABITATS

Variables	Territorial habitat	Nesting microhabitat	*t*-test[a]
GRASS	38.95 (19.94)	23.18 (17.63)	3.79
GENI	11.66 (09.40)	4.43 (06.77)	2.16
JUNI	9.17 (14.72)	1.56 (06.45)	4.31
SH.CO	23.75 (16.24)	9.90 (15.85)	5.37
BARE	38.75 (13.77)	21.61 (17.96)	3.39
ROCK	28.13 (15.24)	56.21 (16.10)	7.85
LITTER	17.71 (14.22)	11.45 (11.01)	2.42
HIT.$\bar{X}$	3.00 (01.84)	1.51 (01.43)	3.06
MAX.H	30.00 (16.94)	10.00 (08.04)	6.52
DIV.I	4.27 (02.16)	1.77 (01.10)	6.61
HET.I	6.45 (03.09)	6.80 (04.52)	0.42

[a] All *t*-values are significant at $P < 0.05$ except HET.I.

Statistical analyses were carried out using the paired *t*-test and stepwise discriminant function analyses (DFA). Data were tested for statistical assumptions of these analyses. The variables were transformed prior to the statistical analyses: the arcsine transformation ($x = \arcsin[\sqrt{x/100}]$) was used for variables expressed as percentages, and the logarithmic transformation ($x = \log[x + 1]$) was applied to the remaining ones. The BMDP statistical package (Dixon 1983) was used for all analyses.

Of the 24 Common Wheatear nests found, 22 were tucked under loose rocks on the ground surface, and two were hidden in excavated holes beneath semi-buried rocks. The rocks covering the nest were all more or less similar size (height = 20.1 ± 11.1 cm, length 90.0 ± 26.9 cm, width 66.2 ± 23.2 cm, [$\bar{x}$ ± SD], N = 22) and the nest themselves were situated at a distance of 30.9 ± 17.1 cm from the outer edge of the rock.

Of the 11 variables compared, only HET.I was not statistically different between the nesting microhabitats and the samples of the territories (Table 1). The values of the cover and structure of the vegetation were in the territory, as a whole, higher than those of the microhabitat surrounding the nesting sites. In fact, only for the variable ROCK were the values for the nesting sites higher than those of the territory.

I performed stepwise discriminant function analysis of a matrix of 11 variables and 48 samples, the latter representing the 24 samples relating to the nesting-site microhabitat and the 24 samples of the nearby patch of territory. The analyses included the variables ROCK, MAX.H, and HIT.$\bar{X}$ in the discriminant function, identifying them as those which best differentiated between the nesting microhabitat and that of the territorial habitat. The discriminant function correctly classified 89.6% of the cases to their corresponding group. Thus, both univariate and multivariate analyses reveal that the Common Wheatear chooses particular microhabitats for nesting that differ from other nearby patches within the territory.

The Common Wheatear in the Sierra Nevada makes its nest on the ground beneath a rock, and the size of these rocks is relatively uniform. Similar specific nest-site requirements have been reported for other birds that nest in scrubland (cf. Petersen and Best 1985a, b; Parker 1986; Martin and Roper 1988). Furthermore, a statistical comparison shows clearly that the nature of the microhabitat immediately surrounding the nest site differs significantly

from that of the territorial habitat, and it is likely that the mating pair use all these different elements as proximate factors in their choice of nesting site. The biological significance of those preferences is that the rocky microhabitats conceal the nest from predators (see also Martin and Roper 1988).

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Gull-billed Tern predation on a Least Tern chick.—During July, 1988, I often saw two Gull-billed Terns (*Sterna nilotica*) flying back and forth through the Least Tern (*Sterna antillarum*) colony of approximately 1500 pairs in Gulfport, Harrison County, Mississippi. On 13 July, one Gull-billed Tern, searching along the water's edge, swooped down and picked up a 7-to-10-day-old Least Tern chick. It landed 70 m down the beach where it swallowed the chick head first. It appeared to have some difficulty handling its prey, taking a couple of minutes to shake the chick and position it. Only one adult Least Tern harassed the Gull-billed Tern. The diet of the Gull-biiled Tern primarily consists of insects, but also includes fish, amphibians, reptiles, crustaceans, earthworms, small mammals, and nestling birds. Rohwer and Woolfenden (1968) reported that the diets of six Gull-billed Terns nesting in Gulfport, Florida, included green anoles (*Anolis carolinensis*). Pellets from a population at Ivanhoe, New South Wales, primarily consisted of mice, although a few contained feathers from Hoary-headed Grebe (*Poliocephalus poliocephalus*) chicks (Hobbs 1976). Other avian

prey have been reported, including young Skylarks (*Alauda arvensis*) (Jensen cited in Bannerman 1962) and young Avocets (*Recurvirostra avosetta*) (De Waard 1952). Although Least Terns have never been reported as prey of Gull-billed Terns, cannibalism has been reported. Gull-billed Terns on the islands of Sivash of the Soviet Union were observed cannibalizing small chicks; they fed these chicks to their own young. Zubakin (1975) suggested this was a method of population regulation. Other than this report, Gull-billed Terns previously had not been reported to prey on a member of their own genus.

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A new record of the Buff-breasted Flycatcher from Nuevo Leon, Mexico.—On 1 April 1984, during an ornithological field trip (Facultad de Ciencias Biologicas, U.A.N.L., Mexico), a male Buff-breasted Flycatcher (*Empidonax fulvifrons*) was collected in Ejido La Chona, Aramberri, Nuevo Leon, Mexico (24°20′12″ N, 99°54′42″ W) west of the Sierra Madre Oriental. This is the first record of *Empidonax fulvifrons* from Nuevo Leon, Mexico (AOU 1983, Check-list of North American birds, 6th ed., American Ornithologists' Union, Washington, D.C.; Cotera and Contreras Publ. Biol., FCB, U.A.N.L., Mex., 2 [1]: 31–49, 1985; Gracia and Contreras Mem., IX Cong. Nac. Zool., Mex. 2:145–149, 1988. The specimen has been deposited in the Coleccion de Aves, Laboratorio de Herpetologia y Ornitologia, Facultad de Ciencias Biologicas, Universidad Autonoma de Nueva Leon (U.A.N.L. 1671). The specimen appears to represent the subspecies *E. f. pygmaeus,* based on measurements (wing chord 60 mm; tail 50 mm, bill 9 mm, tarsus 13.5 mm). A. R. Phillips (pers. comm.) notes the plumage of this specimen is very deteriorated, and he questions the confirmation of the subspecies. We believe the bird is *E. f. pygmaeus* because Ely (Condor 54:34–39, 1962) collected four specimens of *E. f. pygmaeus* from 11 mi east of San Antonio de las Alanzanas in Coahuila, near the border of Nuevo Leon. He mentioned this subspecies was a rare transient in other areas. This place is west of the Sierra Madre Oriental and near to our site. Both places are in the same physiographical region. If our identification is correct, the record is the eastern known record of *E. f. pygmaeus* from Mexico.—Armando Jesus Contreras-Balderas and Jose Ignacio Gonzalez-Rojas, *Laboratorio de Herpetologia y Ornitologia, F.C.B., U.A.N.L., Apartado Postal 425, San Nicolas de los Garza, N.L. Mexico. 66450.* *Received 28 Dec. 1988, accepted 8 June 1989.*

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Brewer's Blackbird parasitizes Tree Swallow.—On 16 May 1988, at the Creston Valley Wildlife Management Area in southeastern British Columbia, I found a freshly laid Brewer's Blackbird (*Euphagus cyanocephalus*) egg in a nest box. The egg was compared to Brewer's Blackbird eggs in nearby nests and matched closely both in color (green-blue with irregular brown splotches) and size (5.1 g). A pair of Tree Swallows (*Tachycineta bicolor*) were occupying the box (i.e., defending against conspecifics) at the time and had completed nest building several days earlier. On 17 May, the resident female swallow laid the first egg of a six egg clutch. I visited the nest next on 6 June, and found six one-day old swallows (mean mass = 2.7 ± 0.3 g [SD]) and one young blackbird (mass = 11.4 g). On 13 June, the young swallows were alive but the blackbird chick was dead. The parasitized swallow nest was located near a loose colony (N = 9 pairs) of Brewer's Blackbirds. First egg dates for the two species in the Creston area are similar: Tree Swallow, 5 May (unpubl. data); Brewer's Blackbird, 7 May (Butler et al. 1986, The birds of the Creston Valley and southeastern British Columbia, Canadian Wildlife Service Occasional Paper No. 58). In addition, both species have incubation periods lasting 12–14 days (unpubl. data; Butler et al., loc. cit.). Intraspecific nest parasitism has not been reported previously for the Brewer's Blackbird. It is surprising that a cavity-nesting Tree Swallow was chosen as a host, as Tree Swallows defend their nests vigorously, especially just prior to egg laying. In addition, the entrance hole to the nest box was only 37 mm in diameter and extended for approximately 75 mm.

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ORNITHOLOGICAL LITERATURE

THE BIRDS OF AFRICA. Vol. III. Edited By C. Hilary Fry, Stuart Keith, and Emil K. Urban; illustrated by Martin Woodcock and Ian Willis. Academic Press, Inc., San Diego, California. 1988:xvi + 611 pp., 32 color plates, numerous line drawings and maps. $129.—Reviewing a mid-series volume of a smashingly successful series puts one in a pickle. What superlatives can you use that haven't already been used? What nuance that contributes to the value of the series has not been mentioned? My first comment comes from the heart . . . Wow! It is difficult to comprehend the magnitude of the job of tying together the bits and pieces of our knowledge of the avifauna of a continent that is so politically fragmented, so ecologically diverse, and so unevenly studied.

Volume III covers the parrots, turacos, cuckoos, owls, nightjars, swifts, colies, kingfishers and their allies, and woodpeckers and their allies. The turacos are treated as a separate Order, the Musophagiformes. Sixteen authors contributed to the volume.

Aside from its use as the major reference on African birds, I have found the "Birds of Africa" to have outstanding, up-to-date, encapsulated accounts of the Orders, Suborders, and Families of birds. At once they provide salient biogeographic information along with morphological, physiological, ecological, and behavioral characteristics which unite the taxon and separate it from other taxa.

Out of curiosity, I compared this volume with Volume IV of the "Handbook of the Birds of Europe the Middle East and North Africa" (Cramp et el. 1985, Oxford University Press, New York). There is considerable overlap in the Orders covered and the birds of North Africa are included in both. Both are monumental accomplishments. Among the differences, "The Handbook" includes sonograms and plates of eggs; "Birds of Africa" does not. Such material is simply unavailable for too many African species. The species accounts in "The Handbook" are generally more comprehensive, again probably reflecting availability of material. "The Birds of Africa" is much more pleasing, with margins nearly double and line drawings much larger. The "Handbook" includes maps of a smaller scale, but the addition of color facilitates their interpretation. Although the shading conventions in "The Birds of Africa" are sometimes confusing, I found the maps superior. One of the frustrating discoveries in comparing these volumes is the level of disparity in range maps for the same species. Comparison of range maps for nearly 20 species revealed no pair that matched!

One of the features I find most useful in "The Birds of Africa" is the completeness and arrangement of the bibliographic citations. The abbreviated, titleless, jam-packed style of the bibliography of "The Handbook" (and also "The Handbook of North American Birds" [R. Palmer, ed., Vols. 4 and 5, 1988, Yale University Press, New Haven, Connecticut]) may include all that is absolutely needed, but is a nightmare for researchers to deal with.

An excellent bibliography of acoustic references to the species included presents not only the citations, format, and sources, but also references to published errata. A list of recordists and the institutions in which their work has been deposited will greatly aid future researchers.

One of the goals for "The Birds of Africa" has been to provide some standardization for common names of African birds—a goal certainly worth pursuing and made possible by the comprehensiveness of the effort. Both English and French names are provided, including alternative English names that are in use. For the species of North Africa, however, I found several differences in both English and French names between "The Birds of Africa" and "The Handbook." Is there no hope?

In general, I found the plates in "Birds of Africa, Vol. III" to be superb—accurate portrayals of species, often with geographic, sex, and age variants shown. Most are shown in more "life-like" postures than provided by utilitarian field guides. The plates are uncluttered with

text, necessary interpretive material appearing on outlines of the birds on the facing page. Line drawings never seem to be mere decoration or filler, but instead illustrate species behavior or anatomy.

Shortcomings of this volume are minor and largely in the realm of literature review and readability. The bibliography is divided into "General and Regional References," and references to each family of birds included in the volume. Although the Introduction states that "The literature has been thoroughly reviewed up to August 1986," literature citations for some groups include few references that recent. This may be due to past research emphasis on some taxonomic groups and lack thereof for others, and perhaps to some extent uneven coverage by authors in this volume. The range of bibliographic coverage is great. For example, there are 191 references for the 25 species of Cuculidae that occur in Africa, 157 for 23 species of Apodidae, 13 for the three species of Trogonidae, and 34 for the 30 species of Picidae. The latter, however, were recently chronicled in Short's monograph on the woodpeckers of the world (1982. Delaware Mus. Nat. Hist. Monogr. 4).

Problems with readability are a result of the necessary attempt to maximize information content in a minimal space. Accepting this as a necessary evil, one still wonders why a single paragraph should contain some perfectly good English sentences and some detached phrases that, with insertion of a proper verb would have been so much more palatable. For example, on p. 1, the last paragraph in the description of the Family Psittacidae begins with the sentence (?) "Popular cage birds, traded legally and illegally around the world, exotic species often becoming naturalized." The paragraph ends with a good, four-line complex sentence.

A page of errata details problems found in previous volumes. Many of these were errors of omission, but the two most common types of errors are ones involving inaccuracies in reported ranges and inaccuracies in plumage or posture shown in plates.

Volume III completes the coverage of non-passerines and puts our knowledge of African birds onto a peak. It is not all downhill from here, but certainly ornithologists working in Africa or with African birds will have an easier go of it for some time to come. Gains in our knowledge of African birds should pick up momentum, because we now have a continent-wide view, summaries from which to begin, statements of deficiencies, and the groundwork laid out for hundreds of research directions. The inspiration is there and the need is so apparent. We must continue our quest for understanding of the African avifauna, because only through such understanding can we hope to have an influence on the future of Africa's natural ecosystems.

The authors, editors, and publisher are all to be congratulated. I look forward to volumes IV to VII!—Jerome A. Jackson.

Songs of Mexican Birds. Taped and produced by Ben B. Coffey, Jr. and Lula C. Coffey. Two cassettes, ARA 13-1 (137 species), ARA 13-2 (109 species). ARA Records, 1989. $21.00 postpaid from ARA, P.O. Box 12347, Gainesville, Florida 32604-0347.—The Coffeys began working in Mexico in 1946, and this extensive series of recordings is a fitting tribute to their time in the field. The impressive total of almost 250 species comprises a representative cross-section of Mexican birds, arranged in the most recent (1983) AOU sequence. The quality of the recordings varies but is generally good. One must remember, however, that in the early days, recording equipment was not at the sophisticated level of today. Domestic sounds, ranging from chainsaws to children, are often audible in the background but convey some of the character of Mexico. Interestingly, the second cassette concludes with vocalizations of a "burrowing frog" and howler monkeys, hinting that non-avian sounds can also be of interest. Many visitors to the Neotropics, myself included, would

find correctly identified "bird-like" vocalizations, particularly of frogs and nocturnal mammals, extremely valuable.

Ninety-two of the species are found on other ARA records, and a further 35 are on L. Irby Davis' "Voices of Mexican Birds." Others can be found elsewhere, but this still leaves a significant number of species whose voices have not previously been readily available. However, I noted some misidentified species: the "Acorn Woodpecker" (*Melanerpes formicivorus*) sounds like a Pale-billed Woodpecker (*Campephilus quatemalensis*) or possibly even a squirrel; the "Streaked Flycatcher" (*Myiodynastes maculatus*) is an example of the calls of Sulphur-bellied Flycatcher (*M. luteiventris*)—the Sulphur-bellied Flycatcher is its dawn song; and the "Lazuli Bunting" (*Passerina amoena*) is a Blue Bunting (*Cyanocompsa parellina*). The "Scrub Euphonia" (*Euphonia affinis*) sounds like a Yellow-throated Euphonia (*E. hirundinacea*); however, euphonias have extremely varied songs, and I cannot be certain the cut is misidentified. The "Yellow-headed Parrot" (presumably referring to *Amazona oratrix*) is from Arriaga, Chiapas, which, on geographic grounds, makes it a Yellow-naped Parrot (*A. auropalliata*).

The cardboard inserts accompanying the cassettes are rather spartan—scientific names are not given, although A.O.U. names are not always used. The most confusing name is "Warbling Chat"; in the narration, four alternative English names are given but, remarkably, none of them is the widely used Gray-crowned Yellowthroat (*Chamaethlypis* [=*Geothylypis*] *poliocephala*). An addendum clarifies the authors' nightjar nomenclature; I can confirm, based on personal field work in February 1989, the voices of Yucatan Poorwill (*Nyctiphrynus yucatanicus*) and Yucatan Nightjar (*Caprimulgus badius*) *are* "Will" and "Ree-o-ree" respectively, as has been recently suspected.

Unfortunately, localities are infrequently and inconsistently given, and dates not at all. In some cases where localities are noted, one might be misled to conclude significant geographic variation. Conversely, locality data would be helpful in cases where vocalizations do vary geographically, including some where incipient species may be involved, e.g., Brown Towhee (*Pipilo fuscus*). The "Cookacheea" or Buff-collared Nightjar (*Caprimulgus ridgwayi*) from Puente Nacional, Veracruz, is the same cut as that on the ARA Records nightbirds cassette (released 1980) but the geographic significance of the record (c.f. AOU 1983), assuming correct labeling, appears to have been overlooked before this review.

Most background vocalizations are left unidentified, and in a few cases, this could lead to confusion by persons unfamiliar with some of the species. Distinguishing songs from calls would also be useful—the narration (at times hard to understand) could be lengthened at the expense of deleting familiar North American birds such as Great Horned Owl (*Bubo virginianus*) and White-crowned Sparrow (*Zonotrichia leucophrys*).

Despite these points, "Songs of Mexican Birds" is an excellent compilation and should be well received as a valuable addition to the growing selection of recordings dealing with Mexican and Neotropical birds.—Steve N. G. Howell.

A Distributional Survey of the Birds of the Mexican State of Oaxaca. By Laurence C. Binford. Ornithological Monographs No. 43. 1989. 418 pp., 28 black-and-white photographs, 3 maps. $40.00 ($36.00 to AOU members) + $2.00 p&h.—Oaxaca probably hosts the largest and most diverse avifauna of any Mexican state. This work (hereafter "Birds of Oaxaca") is a comprehensive and well presented treatment of the 680 or so species Binford lists for Oaxaca. Following the introduction, mainly outlining the history of ornithological work in Oaxaca, are extensive discussions of general physiography, climate, and habitat. The species accounts, arranged in 1983 AOU sequence, include notes on abundance, dis-

tribution, habitat, evidence of breeding and taxonomy; a list of hypothetical occurrences follows the main list. Then come analyses of the breeding avifauna (by habitat) and of migrants (external and internal). A list of Oaxacan type localities, an exhaustive gazetteer, acknowledgments, literature cited, and an index complete "Birds of Oaxaca." A fold-out map inside the front cover shows the distribution of the major habitats within Oaxaca. The map of selected localities is logically placed with the gazetteer where, oddly, one also finds the map of physiographic features which would be better placed with the discussion of general physiography.

The progenitor for this work was Binford's 1968 Ph.D. dissertation, "A Preliminary Survey of the Avifauna of the Mexican State of Oaxaca," and it is pleasing to see the way that "Birds of Oaxaca" has built upon the earlier work. Binford's working knowledge of Oaxacas's complex biogeography is probably unequalled, and his division of the state into physiographic regions is done well. This understanding, often lacking in similar works, forms a solid basis for explaining species' distributions. Perpetuated errors common to other works, including the 1983 AOU checklist, have been thoroughly researched and clarified, e.g., the true distribution of Green Parakeet (*Aratinga holochlora*). The amount of unpublished data brought together in this work is remarkable and touches upon many little-known points, such as local movements of hummingbirds and other supposedly resident species. Importantly, when uncertainty exists, Binford points this out in the hope of stimulating further research.

Given the nature of planning the species accounts, only ten lines devoted to defining relative abundance are disappointing. While I fully appreciate the problems involved with this aspect of any such work, I feel the user deserves some indication of what one might interpret from "fairly common, uncommon, very uncommon," etc.

Both specimen data and sight records were used, but somewhat inconsistently. While rightly casting doubt on data attached to Mario del Toro Aviles specimens, Binford includes Slate-colored Seedeater (*Sporophila schistacea*) in the main list (although admitting strong reservations about the record). Sight records, even those supported by photographs, are problematical, and I understand the desirability of restricting their use to cases involving oneself and personally known observers. However, I see little difference between Slender-billed Wren (*Hylorchilus sumichrasti*), placed in the main list and Flammulated Owl (*Otus flammeolus*) considered hypothetical. In the same vein, the work suffers considerably from Binford not having contacted those birders and field ornithologists who regularly visit Oaxaca. I found numerous cases where the distributional data could have been significantly supplemented had other observers been contacted. For example, for Barred Parakeet (*Bolborhynchus lineola*), which many observers have found "common" (I have even made good tape recordings of its calls) in cloud forest above Valle Nacional, Binford has no "acceptable" records in Oaxaca, or Dwarf Vireo (*Vireo nelsoni*) which is fairly common in Oaxaca Valley 100 km or so to the southeast of Binford's range limit.

I found no mention of the problem of cage birds, although Oaxaca City is a large center for this activity. Binford considers neither Clay-colored (*Turdus grayi*) nor Rufous-backed (*T. rufopalliatus*) robins as reliably recorded in Oaxaca Valley, casting doubt on a nest of the latter species found by Rowley in Oaxaca City. At least in the 1980s, and probably before then, populations of both robins and other cage birds existed (irregularly?) in Oaxaca Valley, and it seems likely that escapees are responsible for such distribution anomalies.

As with any work of this magnitude, one can always find minor discrepancies, e.g., while Streaked Flycatcher (*Myiodynastes maculatus*) is correctly listed as a summer resident on p. 331, in the species accounts the possibility of it being a permanent resident is mentioned, but with no indication as to why that might be the case. The few erroneous statements, usually in relation to areas outside Oaxaca, are understandable, given what little recent, relevant published information exists. For example, stating that Slate-colored Seedeater is

believed to be sedentary, whereas it is notably nomadic, at least in southern Central America (F. G. Stiles pers. comm.; Ridgely, R. S. 1976. "A Guide to the Birds of Panama." Princeton Univ. Press, Princeton, New Jersey). The work is well produced and typographical errors are rare.

"Birds of Oaxaca" is arguably the most comprehensive distributional treatment of any avifauna south of the U.S. border. As well as recommending it highly to all interested in Mexican and Neotropical birds, not to mention North American migrants, anyone undertaking a distributional survey can learn much from Binford's thorough approach.—Steve N. G. Howell.

The Atlas of the Breeding Birds in New York State. Robert F. Andrle and Janet R. Carroll (eds.). Cornell University Press, Ithaca and London. 1988:551 pp., 250 maps, 242 black-and-white illustrations. $29.95. Eight plastic map overlays for an additional $9.95.—The introduction to the volume presents a surprisingly skimpy overview of the data collection process in New York. Anyone seeking detailed information on how to set up an atlas should consult Laughlin et al. 1982. *Amer. Birds* 36:6–19. The New York project differs, regrettably, from all other U.S. projects by using a metric state transverse Mercator grid. Block maps were produced by cutting and pasting together N.Y.D.O.T. Quad sheets which lacked vegetative features. Hopefully the next generation of New York atlasers will adopt USGS topographic maps which are the standard for the rest of the country and readily accessible. Contrary to the introduction, data printouts in at least 50 blocks in two different regions of the state were not checked by field observers for accuracy. The example data sheet includes several codes used with inappropriate species according to standard guidelines. While relaxing standards for breeding confirmation on common species is not a capital offense, a more grievous modification in the original study plan occurred mid-project when efforts to achieve prespecified levels of coverage and confirmation were dropped. Consequently, only two of ten regions of the state averaged over 75 species per atlas block. Nonetheless, some coverage was achieved in 5323 atlas blocks, of which only 337 had fewer than 50 species recorded. The average number of species found statewide was 68. My experience in the western Catskills and Finger Lakes indicates that 110 to 120 species could be found, given moderate habitat diversity and several years intensive coverage. From this book one cannot determine which blocks got such coverage.

The introduction presents eleven maps, all without scales, of political, climatic, physiographic, vegetative and coverage data. Most of these same data are presented in the acetate overlays. The listing of Federal and state wildlife areas on Map 2 is incomplete. At least three of the eleven potential forest types (Map 6) virtually are indistinguishable, and unless the reader is familiar with eighteenth-century canals, there is little chance that the unlabeled river systems (Map 5) will be decipherable. The forest cover map (Map 7) bears scant resemblance to that published in the 1978 N.Y. Forest Resources Assessment.

Species accounts (by 19 different authors) form the bulk of the book. Although all 238 species are indexed, there was no list of families or subfamilies in the table of contents. One must plod through nearly 500 pages of text and maps to locate individual accounts. Each species account is accompanied by a line drawing which consumes one quarter of the page dedicated to text. On the facing page is the atlas map presenting the occurrence of possible, probable, and confirmed breeders as determined during the six year survey. These maps present, in as much detail as one can cram in at 225 blocks to the square inch, the apparent distribution of the species. The reader is cautioned against taking literally the absence of any species from a given block. Remember, coverage varied tremendously, and even if standards for adequate coverage (e.g., 75 species recorded) were met, 30% of the species

may still be undetected. Data around Long Island and Lake Champlain were difficult to decipher because the base map was excessively detailed.

A discussion of each account exceeds the space limitations of this review. As is usually the case in such a multiple-authored compendium, individual accounts vary considerably in style and quality. Each reader will doubtless have his favorites. Each account attempts to review habitat preferences, summarize scanty historical distribution data, discuss the atlas map on the facing page, and present the breeding ecology of the species. Many were interesting and informative, while others were barely adequate. A few general comments may be warranted. The use of 11 subjective abundance categories applied by 19 authors defies reason. Many accounts were woefully short, some barely a half page in length, others much less. A few did little more than summarize the material presented in John Bull's "Birds of New York State" published in 1975 but recently reprinted. I was astonished to see that no one cited E. H. Eaton's paper "Birds of New York 1910 to 1930" which discusses population changes over those twenty years, although some account authors obviously put considerable effort into the historical review. Few New York breeding data are presented, and for the majority of species, the interested reader cannot learn how many eggs the bird normally lays, much less its breeding behavior. Admittedly, other sources of this information exist, but should a reader of a book professing to be about the breeding birds of their state be forced to look elsewhere for such basic information?

In general the accounts are well edited, although individual authors' styles continue to shine (or in some instances, glare) through the editorial veneer. The editors are to be commended for their efforts, but I can't help wondering why define "BP" (before present) as Pre-1950 or split the hybrid Blue-winged × Golden-winged warbler account mid-sentence mid-page?

The first Appendix "The Ecoregions of New York State" presents a good overview. The second, "Natural and Cultural Ecological Communities of New York State" presents 213 undefined habitat categories and belongs elsewhere. It is far too fine-grained to characterize areas the size of atlas blocks. My biggest disappointment, however, was the Breeding Season Table which professes to represent New York data but is actually comprised of many out-of-state sources. It is impossible, for instance, to determine whether reproductive dates listed for any species are representative of New York or even the northeast. Misleading information is rampant in the table. I know of no documented instances of second broods in New York or adjoining states of perhaps 40 species so listed. Wood Thrushes are unlikely to feed themselves at 10 days of age.

The nineteen-page reference section reflects the effort some authors put into researching their accounts. The final listing of over 4300 volunteers who devoted over 200,000 hours to the field effort may give less populated states pause for thought before embarking on a total coverage atlas effort. Forty states and provinces currently are undertaking or have completed bird atlas projects. Compilers of these atlas projects are faced with very similar problems (e.g., finite budgets, need to publish in a timely manner, and desire to provide their audiences with comprehensive analyses). Producers of future atlas books may wish to consider whether it is necessary to duplicate the approach taken by these authors in presenting their mapped data.

This volume, for all its shortcomings, will be an important addition to the literature on New York's birds. Certainly former New York atlas workers will want to have a copy, but the state bird book of choice for many will continue to be John Bull's recently reprinted "Birds of New York State".—Douglas P. Kibbe.

ATLAS OF WINTERING NORTH AMERICAN BIRDS: AN ANALYSIS OF CHRISTMAS BIRD COUNT DATA. By Terry Root. Univ. of Chicago Press, Chicago and London. 1988:312 + xxiv pp., 11 transparent overlays, 42 line drawings, 17 numbered figures, and maps for 346 species. Hardcover $60; softcover $35.—This is a very difficult book to review. To illustrate the point, there are two reviews in the Spring 1989 issue (Vol. 61) of *The Loon* (Minnesota's state bird journal), one glowing and one steaming. I agree with both of them to some extent. Luckily, reviewers are given two hands ("on the one hand"; and "on the other hand"), and I will write a two-handed review.

The author is interested in the factors that limit the winter distribution of North American birds and in the factors that determine centers of abundance for these species. She has recently published two scientific papers on the topic (T. Root, 1988, Ecology 69:330–339; T. Root, 1988, *J. Biogeog.* 15:489-505). In her scientific papers, she concentrated almost entirely on environmental factors such as temperature, precipitation, elevation, and potential vegetation. The atlas can be viewed as a summary of the raw data for her two papers; however, she accurately recognized that there would be a wider audience for descriptive information about the ranges and relative abundances of North American birds than there would be for her scientific papers. Thus, the atlas represents Root's attempt to present her species-by-species analyses to a general birding audience.

Root's introduction describes her methods of analysis, concentrating on how the maps were made and what their limitations might be. The bulk of the book consists of one or two maps for all species that were frequently encountered on Christmas Bird Counts (CBCs), accompanied by a written account for each species. The text describes centers of abundance, discusses factors that are correlated with range limits, and introduces some information about the winter ecology of each species, along with a few miscellaneous tidbits. In the tradition of the breeding bird atlases that are beginning to proliferate, Root has included 11 transparent overlays so that the reader can personally examine correlations between the distribution and abundance of particular species and various environmental factors.

At this point it is necessary to acknowledge a few weaknesses in the book. First, it is based on data that are 17–26 years old. Second, it provides a static picture of winter ranges by providing only a single map for ten years of data. Some species *do* have relatively static winter ranges, both from year-to-year and over the past 26 years. For those species, these maps will be most useful. However, a number of species are more dynamic, either from year-to-year (irruptive species and weather-sensitive species) or over the past 26 years (House Finches [*Carpodacus mexicanus*] in the east are perhaps the best example). Root extensively discusses some of the problems with the maps in the introduction, and she attempts to deal with those problems by relegating maps for 96 of the 346 species to an appendix. However, I think every individual would probably make different decisions as to which species to put in the appendix and which to keep in the body of the text. The problem is that there are *both* important weaknesses and useful information in the maps for all 346 species. Let the reader beware!

Perhaps the most basic issue is the appearance of the maps. Most of you have seen the advertising circular for the book and can judge for yourselves. In a word, the maps are not easy to read. The two-dimensional maps would be improved by using black for the highest density areas and shades of gray (or cross-hatching) for areas with intermediate density. I am now used to the two-dimensional maps, and I can get a lot of information from them; however, I still am not used to the three-dimensional maps. The two biggest problems with the three-dimensional maps are that: (1) the peaks of the maps are displaced away from the centers of abundance enough that you can't tell from these maps where the centers of abundance are, and (2) the maps include cross-hatching even in areas where the species is absent, providing little contrast within the maps.

I also have some problems with the criteria involved in deciding where the limits of the ranges are. To my mind, determining limits of ranges should be entirely separate from determining centers of abundance. The limits of ranges should be determined from frequency of occurrence data. For most species, there will be a number of CBC locations that never recorded it; and for many species, there will be some locations that recorded it every year. In between, there should be a number of locations that recorded the species some years but not others. It would be very useful to see a graph for each species showing how often CBC locations fell into each of these categories. It is this information on frequency of occurrence that should be used to determine a range boundary. Instead, Root used information derived from measures of relative abundance. (The range boundary is defined as the line connecting points at which the abundance is calculated to be 0.5% of the maximum abundance. Maximum abundance is defined as the lowest average value for a CBC location that is greater than 99% of the values for that species). The problem with Root's method is as follows: in species with high maximum average abundances at at least 1% of CBC locations, many peripheral locations with a very low abundance may be excluded from the mapped range; however, in species that lack high peaks of abundance, peripheral locations with low levels of abundance will be included in the mapped range.

I think that the contouring algorithm Root used is much better for calculating and mapping relative abundance than it is for calculating range boundaries, but even here there are questions. For example, should a single algorithm be used for species that vary so much in their patterns of distribution and abundance? Perhaps better results would come from using a different algorithm (or a different decision rule using the same algorithm) for the highly gregarious species with enormous peaks of abundance than is used for species that are more thinly spread. It would add a lot to the book if there were graphs for each species showing the frequency of categories of relative abundance for all CBC locations where the species was observed.

The text that accompanies the maps has some problems as well. The heart of the problem for most readers of *The Wilson Bulletin*, I think, is that Root approaches the text as a biogeographer, not as an ornithologist or a birder. For example, she deals poorly with extralimital records (both in the maps and in the text). Extralimital birds should be carefully checked out to see if they are well-documented; those that are well-documented should be represented on maps with a single, small dot. They essentially should be ignored in a text where the main interest is in centers of abundance and range limits. Instead, extralimital records seem to be included with little scrutiny. They have a disproportionate effect on the maps, and they are discussed in the text, sometimes laboriously.

In general, Root provides little evidence that she is aware of identification problems. Maps of Broad-winged Hawk (*Buteo platypterus*), Swainson's Hawk (*B. swainsoni*), and Semipalmated Sandpiper (*Calidris pusilla*) are included in the appendix even though most ornithologists I know believe that the overwhelming majority of these records represent misidentifications. There is no mention of identification problems of accipiters (G. G. Daniels, 1975, *Am. Birds* 29:634–637). I can find no mention of Thayer's Gull (*Larus thayeri*) at all (D. M. Mark, 1981, *Am. Birds* 35:898–900); birders had never heard of it when they collected these data, but it has been officially considered a full species for 16 years. Many records of Herring Gull (*L. argentatus*) and Glaucous-winged Gull (*L. glaucescens*) along the Pacific Coast may actually represent Thayer's Gull. These are all difficult problems to deal with, but they need to be addressed head on in a book of this type.

One of the biggest disappointments of the text is that Root does not have a good feel for the habitat requirements of birds, and she does not differentiate well between potential vegetation and actual vegetation. Thus, for an open-field species like the Vesper Sparrow (*Pooecetes gramineus*), she expresses surprise that it is found in the "mixed mesophytic and

deciduous forest" biome (p. 235), even though much of that forest was cleared for agriculture long ago and remains open today. The problem recurs in the discussions of habitat relationships for a variety of species.

One of the questions a potential reader might have is: Should Christmas Bird Count data be used at all for this kind of project? My answer is an unequivocal "yes." Certainly, CBC data are messy, and that messiness contributes to the problems with this book. But that messiness can be cleaned up quite a bit by careful attention to detail. CBC participants make identification errors; however, the CBC editing system is increasingly able to identify those errors and weed them out (CBC analysts should be able to mimic that process for the older data). Some CBC participants cover their CBC circles in a haphazard way and count individuals in a lackadaisical way; but on a large scale, information about relative abundance should correlate with reality for most species. Effort on CBCs varies dramatically from place-to-place and has increased through time; however, effort has been consistently reported (especially since about 1955) and methods are available to control for effort when analyzing CBC data (C. E. Bock and T. Root, 1981, *in* C. J. Ralph and J. M. Scott, eds., "Estimating Numbers of Terrestrial Birds," *Studies in Avian Biology* 6:17–23; G. S. Butcher and C. E. McCulloch, 1989, *in* J. Sauer and S. Droege, eds., "Proc. of the Workshop on the Analysis of Population Trends from Avian Surveys," United States Fish and Wildlife Service, *in press*). The CBC provides information mostly from the second half of December, when many species are not on their definitive winter ranges; however, there may be no such thing as a definitive winter range for many of these species, since their movements may depend on the severity of winter weather conditions.

As messy as it is, the CBC is the only source of quantitative information on the continent-wide distribution and abundance of winter birds available. A number of studies have correlated CBC data with other sources of data and found general agreement (G. S. Butcher, 1989, *in* J. Sauer and S. Droege, eds., "Proc. of the Workshop on the Analysis of Population Trends from Avian Surveys," United States Fish and Wildlife Service, *in press*). When carefully used, the CBC provides a treasure-trove of information.

I have made some severe criticisms of this book, but what is the bottom line? Should you buy it or should you ignore it? For me, the answer is easy. I *need* this book. I expect to use it almost daily. I may swear at its limitations, and disagree with its maps or text, but there is a tremendous amount of useful information here on subjects that fascinate me. My hunch is that many of you will want this book too and will actually enjoy fighting with it. While doing so, let's give the author credit—she has done a tremendous amount of work to further our understanding of the winter biogeography of North American birds.—GREGORY S. BUTCHER.

ADAPTIVE STRATEGIES AND POPULATION ECOLOGY OF NORTHERN GROUSE. Edited by Arthur T. Bergerud and Michael W. Gratson. Univ. Minnesota Press, Minneapolis, Minnesota 1988:809 pp. $59.50 (cloth). Also available in two volumes, $17.95 each (paper).—The book is arranged in two parts: Population Studies (11 Chapters) and Theory and Synthesis (5 Chapters). Each chapter contains a summary; there is an useful index and a section on references (1104 total) of which the most recent is 1985.

The initial chapters on Population Studies were written by 12 different authors, while the portion on Theory and Synthesis was primarily written by A. T. Bergerud. As expected in a work of this magnitude, the writing is uneven, and some chapters are considerably out of date. Some read like the theses from which they were modified.

This is not a book written by the major grouse researchers, although many of them were

offered the opportunity to contribute. Instead, it contains chapters written primarily by people who have not published extensively. Most chapters obviously have been polished by the editors, and some differ from the original theses. The individual chapters on population studies are interesting, but some are limited and do not represent work throughout the species' range. Much of this work has not been peer reviewed outside of graduate committees and represents gray literature at best. This is a major failing of the entire book.

The Theory and Synthesis chapters represent the major contribution of the book. However, the chapters on Mating Systems in Grouse and Survival and Breeding Strategies of Grouse repeat what is generally known. Somewhat novel and disputed ideas are presented in Chapters 12, 15, and 16. Many readers will be disappointed with the chapter on 10-year cycles of grouse as only D. Chitty's hypothesis is explored. Presumably the authors (Page and Bergerud) disagree with all other hypotheses. Differences between genotypes is further discussed in the chapter on Population Ecology of Grouse where the reader is asked to believe that density-dependent changes in mate choice lead to chicks with differing intrinsic viabilities. Strong evidence for this postulation is not presented. I was also especially interested to learn (p. 731) that hunting mortality is additive to natural mortality over winter. Considerable evidence exists that hunting mortality below some threshold (about one-half of the annual mortality) is compensatory; above this level hunting mortality may be additive. This will be a point of contention with many readers.

Some "grousemigan" researchers will be surprised to see some of their unpublished data in this book even though their unpublished reports may be cited. At least one legal action was reportedly threatened over use of unpublished data while this book was in the early stages of preparation. The editors/authors have been careful to acknowledge everyone whose data they examined or used. Unfortunately, they did not have the permission of everyone for the liberal use of selected data collected by others.

This is not an easy book to digest or fully understand. It is well edited and misspellings are minor (Hoffman, R. S. should be Hoffmann, R. S.). Most tables and figures are understandable although some figures are too complex for quick comprehension. The grouse sketches by D. H. Mossop are pleasant additions to otherwise standard figures.

Despite the obvious biases shown by some authors and the differences in interpretation, "Adaptive Strategies and Population Ecology of Northern Grouse" is recommended for serious students of grouse. It will be a widely read, discussed, and cussed book which will have a prominent place on the desk of active "grousemigan" researchers. There should be ample opportunity for everyone to find something to test in this important contribution to the grouse literature. The editors, especially Tom Bergerud, are commended for seeing this "labor of love" through to completion. The cloth price of $59.50 is high but I recommend the cloth copy over the paper ($17.95 ea for two volumes) as this book will be used extensively.—Clait E. Braun.

North American Owls. By Paul A. Johnsgard. Smithsonian Institution Press, Washington, D.C. 1988:295 pp., 32 color plates, 54 numbered text figs., 19 range maps, 12 numbered tables, 3 appendices. $45.00.—Some will think "not another book on owls!" This, however, is not just another owl book. It is a well-balanced coverage of the biology and natural history of the North American species.

Each of the 19 species is illustrated in color. The Fuertes paintings portraying 10 species are of little value for species identificaiton in my opinion. Fourteen species are pictured in color photographs of mostly good quality.

Johnsgard's book is organized much like Mikkola's "Owls of Europe" (1983). Johnsgard,

however, aimed at a compromise between a non-technical and a highly technical volume, a goal that he clearly achieved. Mikkola's book is more comprehensive with about 40% more citations and 69 tables crammed with useful data.

The text is in two major divisions. First is a section of six chapters entitled "Comparative Biology of Owls." A short chapter deals with the fossil record of owls and several views of owl taxonomy. The chapter on ecology and distribution is strongest in its coverage of habitat and food. The other two subsections, biogeography and species densities, and ecological aspects of body size, are relatively weak. The chapter on morphology and physiology starts with general morphology but is best in the presentation of vision and hearing, two senses very important to owls. Coverage in a chapter on behavior ranges from maintenance behavior through breeding and other social behavior to hunting and prey capture behavior. The chapter on reproduction encompasses population densities, home ranges, clutch data, dispersal, and mortality. The sixth chapter, "Owls in Myth and Legend," although interesting, seems out of place in a book on natural history. Missing from the section on comparative biology is a discussion of sexual dimorphism. This topic, one that has stirred much interest and disagreement among biologists, deserves to be covered in a book of this type.

Several tables are included in these chapters and contain well-organized data. The numerous line drawings illustrating morphology and behavior are mostly well-drawn and useful. Fig. 10, though, which purports to show the relative size of North American owls is highly misleading.

Part two contains chapters on 19 species. Each account provides a range map, list of subspecies, wing, tail, and egg measurements, body and egg weights, description, assistance in identification, vocalizations, habitat and ecology, movements, foods and foraging behavior, social behavior, and breeding biology. A final section in each account covers, curiously, two unrelated topics: evolutionary relationships and conservation status. This section is quite brief for most species, probably reflecting the paucity of information on population status and trends for most owls. Other sections of the species accounts are well-balanced, easily read, and sprinkled with a good sample of references.

There are three appendices: a dichotomous key to genera and species, a description of typical calls of North American owls (with sonograms) organized in groups of similar sounding calls, and a listing of the origin of scientific and vernacular names of owls. A glossary and index are also provided.

In summary, Johnsgard has provided a good, very usable reference to the owls of North America. He writes clearly and provides up-to-date information. Of the numerous books on North American owls, this is certainly the best and most comprehensive. However, the depth of coverage will not satisfy those needing detailed information on many aspects of owl biology. This book is a must for all community, college, and university libraries. Individuals desiring a general treatment of owls will also want it for their personal collections.—Carl D. Marti.

Bird Conservation. 3. Edited by Jerome A. Jackson. The Univ. of Wisconsin Press, Madison, Wisconsin 1988:viii + 177 pp., 11 text figs., 17 tables. Hardcover $17.50, paper $12.95.—*Bird Conservation* is a series published for the United States section of The International Council for Bird Conservation. Each issue features chapters by authorities on an important conservation issue. Topics in Vol. 3 concern the past, present, and future of North American forests and their avifauna. Six forest ecosystems are discussed: ponderosa pine by Jeffrey D. Brawn and Russell P. Balda, the oak-hickory and pine forests of the Ozarks by Kimberly G. Smith and Daniel R. Petit, oak-gum-cypress by James G. Dickson,

Douglas-fir forests of California by Martin G. Raphael, Kenneth V. Rosenberg, and Bruce G. Marcot, southern Appalachian subalpine forests by George A. Hall, and southeastern pine forests by Jerome A. Jackson. Jackson is also the editor of "Bird Conservation." Curtis S. Adkisson presents a chapter on the history of cavity-nesting birds, their present status, and future prospects. All of these authors succeed to various degrees, depending on the information available, in presenting a history of their forest types and the avifauna dependent on each. Brawn and Balda and Raphael et al. limit their assessment of the present status of birds in ponderosa pine and Douglas-fir forests to the results of specific studies that have been made on habitats of known history, while the other authors include a much broader range of information, including their own studies and data from other sources as well. Raphael et al. do not discuss the status of the Spotted Owl (*Strix occidentalis*), presumably because it was not part of their study. This is one of the few disappointments in the book, which provides a lot of valuable information on other species of special concern and their forest habitats.

All of these forest ecosystems have been adversely affected in the past. The forests of the Ozarks were virtually destroyed. Today, they all face a gamut of pressures and threats—urbanization, short rotation harvest schedules, clearcutting and intensive site preparation, removal of snags and dead trees, monoculture tree farming, forest grazing, fire suppression, and air pollution. Adkisson declares that current management plans "amount to disaster for any organism that depends on old-growth forest." He calls for regional ecosystem planning to set aside critical habitat reserves for species with narrow ecological tolerance. He and other authors argue that much longer harvest rotations must be established in critical habitats—as long as 100 years in southern pine forests and more than 200 years in the Pacific Northwest. But this will not be easily accomplished: Jackson maintains that the Red-cockaded Woodpecker (*Picoides borealis*), an indicator species for mature southern pine forest needs 80–400 ha of home range per clan. Since a minimum of six neighboring clans is essential to sustain a population for a decade and perhaps as many as 500 clans may be neccessary to sustain a population indefinitely, an enormous area of pine forest must be specially managed to sustain this species. All of these authorities express concerns similar to Hall's who writes "that we are losing a beautiful ecosystem and that our descendants will never experience the joys of days spent in the cool conifer-covered heights."

Jackson has eliminated the review of bird conservation literature found in previous volumes of this series and replaced it with a single book review. The bird conservation news section amounts to only one short article on "The Status and Conservation of Woodpeckers" by Lester L. Short. It may be that the obvious difficulty the U.S. section of the I.C.B.C. has getting this series published in a timely manner (the most recent references in this issue are not later than 1986 in most chapters) has led to the editor's abandoning any hope of presenting up-to-date news. This is a shame, because the review of bird conservation literature in previous volumes was a valuable service, bringing together in one source references that are difficult to find otherwise. I would like to see this feature reinstated in future volumes. Whether the publishers do this or not, this series will continue to be an important source of information on conservation of North American birds. Vol. 3 is an excellent account of the history, present status, and future prospects of North American forest ecosystems. One could only wish that other important forest ecosystems might be included.—Albert R. Buckelew, Jr.

ACTA XIX CONGRESSUS INTERNATIONALIS ORNITHOLOGICI. Edited by Henri Ouellet. Univ. of Ottawa Press, Ottawa, 1989: Two volumes, 2815 pp., one photo, many black-and-white diagrams and graphs. $175 (Canadian).—If the sheer volume before us is any criterion, ornithology in the summer of 1986 was flourishing. We have here about 10 pounds of "Acta" of the 19th International Ornithological Congress held in Ottawa, Canada, in that year. The proceedings are led off by the Presidential Address of the late Klaus Immelmann entitled "Ornithology—an Interdisciplinary Challenge." This expressed the theme of the Congress and many of the 50 symposia cast rather far afield from traditional ornithology. However, almost every aspect of ornithology as it is practiced today was covered in these symposia, most of which consisted of five papers together with introductory and/or concluding remarks.

In additon to the symposia there are five plenary lectures: "Individual Performances in Sparrowhawks: the Ecology of Two Sexes" by Ian Newton; "Biogéographie evolutive à différentes échelles: l'histoire des avifaunes méditerranéees" by Jacques Blondel; "Genetic Studies of Birds—the Goose with Blue Genes" by Fred Cooke; "The Control of Migration of European Warblers" by Peter Berthold; and "Eco-evolutionary Aspects of Bird Movements in the Northern Neotropical Region" by Mario Ramos. these are thoughtful syntheses of much of the published work of these authors.

There is also an interesting history of Canadian ornithology by Secretary General Henri Ouellet, various reports, and a list of the 1300 or so people who attended. The Statutes and By-laws of the International Ornithological Committee and the list of members of that Committee are included.

Probably no one will read all of the material in these two volumes. Perhaps many people who attended the Congress will use the volumes as I have, in reading the papers I was unable to hear in person. Since the symposia were held in twice daily sets of five concurrent sessions, no one was able to do more than sample the total program. It would be pointless to attempt a detailed review of the contributions but as is typical of all symposia volumes, the papers vary widely in quality and information content. Some will be valuable summaries and references, but others will soon be forgotten. Most are in English but a few are in French.

Not included, even by title, in these Acta are the 150 contributed papers, the 380 poster presentations and the 43 round-table discussions. As these occupied perhaps 40% of the Congress day, people who were not in Ottawa will not feel the full flavor of what was indeed a stimulating meeting.

Clearly the size of these Congresses and the resulting Acta have almost gotten out of hand. It is of some interest to trace the growth of these publications. The proceedings of the Ithaca (1962) Congress had 1246 pages and was the last to include all the papers presented. Subsequent proceedings had only the plenary papers and the invited symposia. The Oxford (1966) Congress produced 405 pages, The Hague (1970), 745, Canberra (1974), 765, Berlin (1978), 1463, and Moscow (1982), 1335. I leave it to the reader to make his own extrapolation of these figures to the Congress of the year 2000. While the Congresses themselves provide a stimulating atmosphere for face-to-face discussion at the international level, it is pertinent to ask if the laborious and expensive task of publishing the Acta is really worthwhile. Not only are many of the papers summaries of work published elsewhere, but the amount of time devoted in editing these accounts is an inordinate burden on the Secretary General who has already labored long and hard to get the Congress off the ground. I understand that the International Ornithological Committee is seriously considering a revision of the publication policies of the Congresses.

In any event Editor Ouellet and his five member editorial committee are to be congratulated on completing the publication task in such fine shape and so promptly.—GEORGE A. HALL.

Also Received

The Popular Handbook of British Birds. (5th revised edition) By P. A. D. Hollom. H. F. & G. Witherby Ltd., London, 1988:xxv + 486 pp., 136 colored, 15 black-and-white plates. (Distributed by David & Charles, Inc., North Pomfret, Vermont). $34.95.—The original version of this book published in 1952 attempted to give a convenient one—volume summary for the amateur birdwatcher of the material contained in the now almost legendary five-volume "Handbook of British Birds" by Witherby, Jourdain, Ticehurst, and Tucker. The present edition attempts to bring matters up-to-date. Each species is treated in a set format, of Description, Habitat, General Habits, Food, Nesting (if it does nest in Britain), and Status and Distribution. These accounts are brief, usually only a page or page and a half, and a third of this space is taken up with a description. These descriptions are almost too brief to be helpful in identification, but each species is figured in a small, colored painting of a style reminiscent of the last century. For most species these are adequate for identification purposes. There is also a good collection of colored plates of eggs. There are no references. The book may be useful to those beginning bird watchers in the British Isles who are interested beyond the stage of simple identification, but it will have a very limited utility for Americans. Visitors to Britain would do better with one of the excellent field guides available.—George A. Hall.

Waterfowl in Winter. Edited by Milton W. Weller. University of Minnesota Press, Minneapolis, 1988:xx + 624 pp., many black-and-white graphs and diagrams. $49.50 (cloth), $19.95 (paper).—In January, 1985, a symposium on the ecological and behavioral aspects of waterfowl in winter was held in Galveston, Texas. We have here a collection of most of the papers that were given at that symposium. As is typical of such symposia, some of the papers could not stand alone or were to be published independently. Elimination of these has produced a volume whose content is above the usual run of symposium proceedings. The volume contains 37 papers and 10 Workshop Summaries from over 100 contributors.

The papers are collected into nine groups: Winter in Perspective; Reproductive and Social Behavior; Activity Budgets; Community and Feeding Ecology; Weights, Molts, and Condition; Habitat Resources and Habitat Selection; New Habitats and Habitat Management; Harvest, Distribution, and Population Status; and Decimating Influences; Habitat Loss, Toxins, and Disease. All told this collection presents a good picture of our present knowledge of wintering waterfowl and some of the problems confronting them and presented to us by essentially all the biologists active in this field.—George A. Hall.

Birds, Birders, and Birding in the Saginaw Bay Area. By Eugene Ellis Kenaga. Chippewa Nature Center, Inc., Midland Michigan, 1983:iv + 132 pp., 16 maps, many black-and-white drawings and cartoons, (Available from the author, 1584 E. Pine River Road, Midland Michigan, 48640). $8.95 + $1.25 shipping.—The tripartite title describes this attractive work completely. After a brief description of the region, the largest portion of the text is devoted to a list of birds of this seven-county area in Michigan's Lower Peninsula together with brief annotations. The customary bar-graphs showing seasonal occurrence are included. The author then draws on his long experience in the area to analyze some of the changes that have occurred. The second section outlines the local birding activities and includes sketches of prominent birders, while the third section describes, with maps, various birding spots in the area. A novelty for this type of publication is the series of cartoons which enliven the whole work. The publication should prove most useful to the local birders as well as visitors to this popular vacation area.—George A. Hall.

Wildlife Reserves and Corridors in the Urban Environment. By Lowell W. Adams and Louise E. Dove. National Institute for Urban Wildlife (10921 Trotting Ridge Way,

Columbia, Maryland, 21044), 1989:vi + 91, many black-and-white photos and diagrams. $7 (paperback).—The subtitle is "A Guide to Ecological Landscape Planning and Resource Conservation."—G.A.H.

Cormorant. An International Journal of Marine Ornithology. Published by the African Seabird Group, % Fitzpatrick Institute, University of Cape Town, Rondebosch 7700, South Africa. $25 per year.—With Volume 16 No. 1, June 1988 the "Cormorant" has expanded its coverage to include the biology of the seabirds of the world.—G.A.H.

The following publications are available from the Publications Unit, U.S. Fish and Wildlife Service, Room 148 Matomic Building, Washington, D.C. 20240.

Fisheries and Wildlife Research and Development 1987/88. Edited by Paul A. Opler. U.S. Fish and Wildlife Service, Denver, Colorado, 1989:iii + 90 pp.—A useful summary of the research activities of the Agency.—G.A.H.

Temporal and Geographic Estimates of Survival and Recovery Rates for Mallard, 1950 through 1985. By Diane S. Chu and Jay B. Hestbeck. U.S. Fish and Wildlife Service Technical Report 20., Washington, 1989:v + 57 pp.—G.A.H.

Premigrational Movements and Behavior of Young Mallards and Wood Ducks in North Central Minnesota. By Ronald E. Kirby, Lewis M. Cowardin, and John R. Tester. Fish and Wildlife Research 5, U.S. Fish and Wildlife Service, Washington, iii + 25 pp.—G.A.H.

INFORMATION FOR AUTHORS

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Authors of accepted papers are urged to submit voucher photographs of their work to Visual Resources for Ornithology (VIREO) at the Academy of Natural Sciences of Philadelphia. Accession numbers from VIREO will then be published within appropriate sections of the paper to facilitate access to the photographs in subsequent years.

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The editor welcomes queries concerning style and format during your preparation of mss for submission to the *Bulletin.*—CHARLES R. BLEM, Editor.

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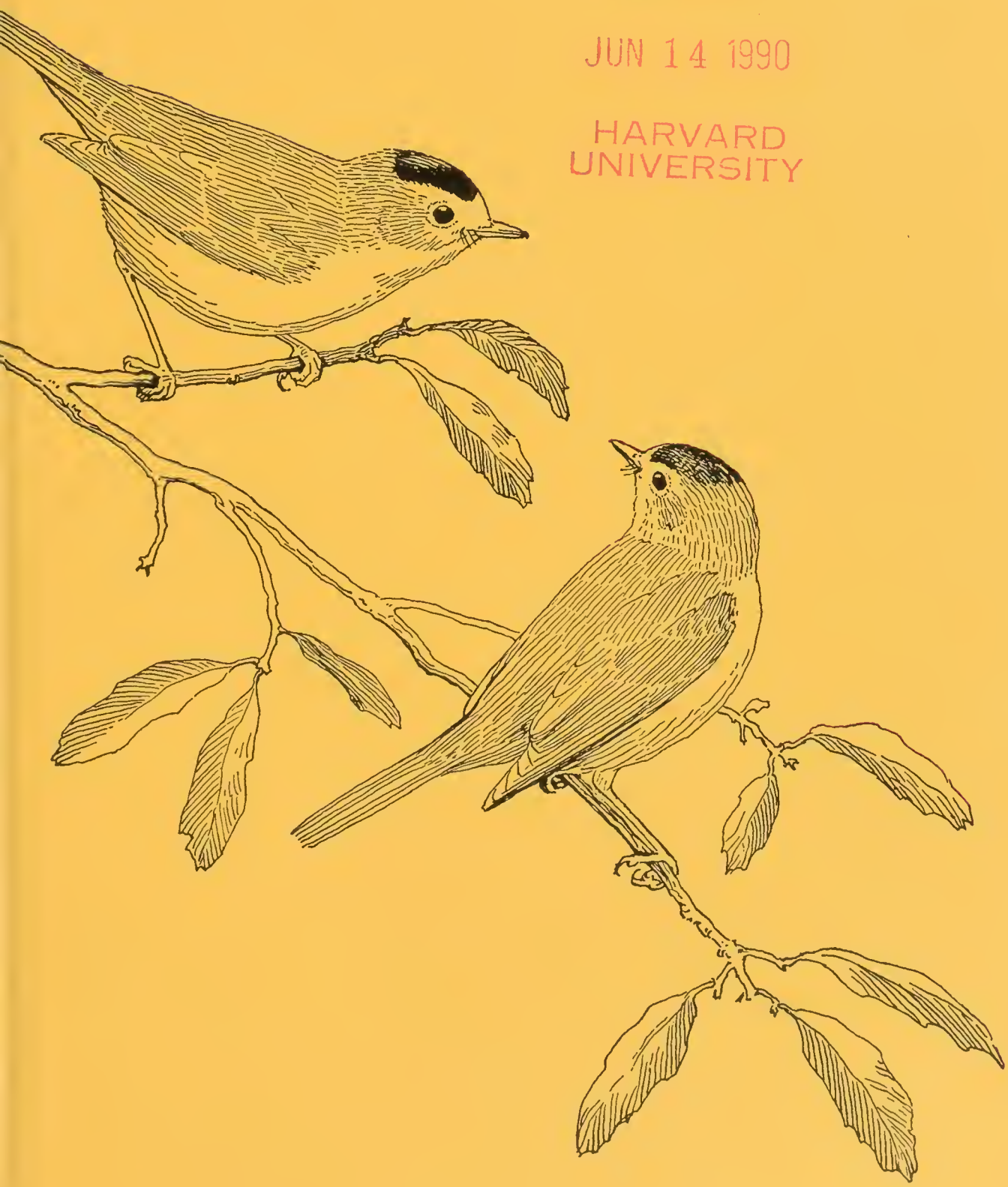

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GEOGRAPHIC DIFFERENTIATION AND DISTRIBUTION OF THE PERUVIAN SCREECH-OWL

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ABSTRACT.—Analysis of vocalizations of the dwarf form of screech-owl from northwestern coastal Perú establishes conspecificity with the Peruvian Screech-Owl (*Otus roboratus*) of the mid-Marañon Valley, a species previously considered to be monotypic. The small coastal form (*O. r. pacificus*) differs significantly from the nominate form in a series of characters of both size and color; some features do not overlap. Both subspecies of *O. roboratus* are polymorphic in color, with gray-brown and red phases represented. Alliance of *O. r. roboratus* with *O. choliba* and *O. r. pacificus* with *O. guatemalae,* as proposed by Hekstra, is not supported by either vocal features or plumage pattern. *Received 7 April 1989, accepted 24 Aug. 1989.*

The arid woodlands of northwestern coastal Perú have long been known to harbor a tiny screech-owl (*Otus*) of dubious systematic affinities. First collected over one hundred years ago, this owl was known in the mid-decades of this century to the late Maria Koepcke, pioneer naturalist in Perú, and has been recorded on a fairly regular basis in recent years by most field groups that have visited the region.

We first became intrigued by the identity of this little owl as a possibly undescribed taxon in 1967, when two specimens were netted in Piura by the late Carl B. Koford and his field party (R. B. Hamilton, R. B. Huey, and F. C. McCullom) from the Museum of Vertebrate Zoology, during a general survey of vertebrates in northwestern Perú. Although the basic color pattern suggested affinity with the Peruvian Screech-Owl (*O. roboratus* Bangs and Noble 1918), the unusually small size indicated that the owl represented an undescribed species. During three visits to Perú

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(August–September 1970, February 1972, and October–November 1974) we were fortunate to obtain additional specimens and tape recordings of the principal vocalizations both of the small owl, in Tumbes and Piura, and of the large *O. roboratus* in the Marañon drainage of Cajamarca and Amazonas.

This report presents the results of morphological, vocal, and ecological analyses which support the view that the small owl from northwestern Perú is a coastal differentiate of *O. roboratus*.

O. roboratus is known in the literature by several different vernacular names: "Roborate Screech Owl" (Hekstra 1973), "West Peruvian Screech-Owl" (Meyer de Schauensee 1966, Parker et al. 1982), "Urcututu occidental" (Koepcke 1964), and "Peruvian Screech Owl" (Marshall and King 1988). We prefer the latter usage (but with a hyphenated group name) because it is brief and appears in a world list of the names of birds of prey that can serve as a formal standard of vernacular nomenclature.

MATERIALS AND METHODS

Study specimens.—The Peruvian Screech-Owl is known at present from approximately 50 specimens. All major collections of the species are in the United States (American Museum of Natural History, New York; Louisiana State University Museum of Zoology, Baton Rouge; Museum of Vertebrate Zoology, University of California, Berkeley). In addition, five institutions (Chicago Natural History Museum; Museum of Comparative Zoology, Harvard University; Museo Historia Natural Javier Prado, Lima; British Museum [Natural History], Tring; and Alexander Koenig Museum, Bonn) have two specimens each. I have examined all of the aforementioned specimens except the type of *O. roboratus* (MCZ, Harvard) and the four skins in Tring and Bonn. Elevations in the following account are those on the specimen tags; as a result some are not in the metric system. Joe T. Marshall kindly provided color slides of the two specimens at Tring. John S. Weske graciously sent measurements of the two specimens at Bonn.

Measurements.—Size of three appendages of study skins was measured in millimeters with a dial caliper as follows: (1) wing (chord) length, from the bend of the wing to the tip of the longest primary; (2) tail length, from the basal point between the insertions of the central pair (1–1) of rectrices to the tip of the longest rectrix; and (3) bill length, from the anterior edge of the nostril to the tip of the upper mandible. We did not measure either the tarsus or the toes because of the difficulty of measuring feathered surfaces. Body mass in grams, was measured with a Pesola balance from each fresh specimen within a few hours after collection. For analysis, values of body mass were used both in raw form and after transformation to cube roots.

Analysis of coloration.—Variation in color of the plumage of the crown and lower dorsum was analyzed quantitatively with a Bausch and Lomb Spectronic 505 recording spectrophotometer equipped with a visible reflectance attachment. Flatness of the 100% line was maintained within limits of 1.0% peak-to-peak, and flatness of the 0% line, within 0.5%. To permit analysis of limited areas of plumage, the sample port was narrowed to a diameter of 22 mm. The background of the contracted hole was painted with Krylon Spray Paint, Number 1602, Ultra Flat Black Enamel, produced by Borden, Inc. From trichromatic coefficients (x, y, z) obtained from curves of percentage diffuse spectral reflectance between

400 to 700 mμ by the 10 selected ordinate method of Hardy (1936:49–51), dominant wavelength (λ_d), brightness (Y), and excitation purity (P_e) were computed according to table 6 of Judd (1933:371) and using the ratios described in Johnson and Brush (1972:247). Routine comparison of series of specimens under uniform lighting which approximates natural north sky daylight was accomplished under a Macbeth Super Color Matching Skylight (Model BX 848A).

Vocalizations.—Trills and barks of owls were preserved for analysis on magnetic tape by use of a Uher Report-L portable tape recorder and a Sennheiser MKH 804 directional microphone. In the laboratory, the vocalizations were displayed visually as audiospectrograms using a Kay Elemetrics Model 6061A 85-8000 CPS Spectrum Analyzer with the wide band setting.

CHARACTER VARIATION

Populations of the Peruvian Screech-Owl can be divided conveniently into those occurring in the Rio Chinchipe-mid-Marañon drainage, between the western and Central Andes, and those inhabiting the arid coastal plains and foothills of northwestern Perú, west of the western Andes (Fig. 1). For the sake of simplicity in the following discussion of character variation, we use the names "Marañon" and "NW coast" or "coastal," respectively, to identify these disjunct populations.

Size.—In wing length, tail length, bill length, and body mass, Marañon specimens average significantly larger than those from the northwestern coast (Table 1). Both sexes illustrate this pattern. In fact, in all characters except bill length, no overlap occurs between values from specimens representing the two groups of populations.

Sexual dimorphism in size.—Using the Dimorphism Index (D. I.) devised by Storer (1966:424), we determined the degree of dimorphism in Marañon birds to be 1.36 in wing length and 3.93 in cube root of body mass. Comparable figures for coastal birds are 0.36 and 0.45, respectively. These D. I. values are low, in keeping with the insectivorous habits (see beyond) of this species. Furthermore, as in three species of North American *Otus,* degree of sexual dimorphism increases with absolute body mass (Earhart and Johnson 1970:255).

Color and pattern.—Birds from populations on either side of the western Andes exist in two color morphs or phases, "gray-brown" and "red" or "rufous." Within either morph, Marañon birds differ subtly from northwestern coastal birds in brightness, dominant wavelength, and purity of both the crown and the lower dorsum (Table 2). Differences in the color variables of the lower dorsum are more pronounced than are those of the crown.

Although both groups of populations clearly show the dark brown or blackish cap and pronounced nuchal collar that characterize the Peruvian Screech-Owl, dorsal or ventral pattern differences between specimens rep-

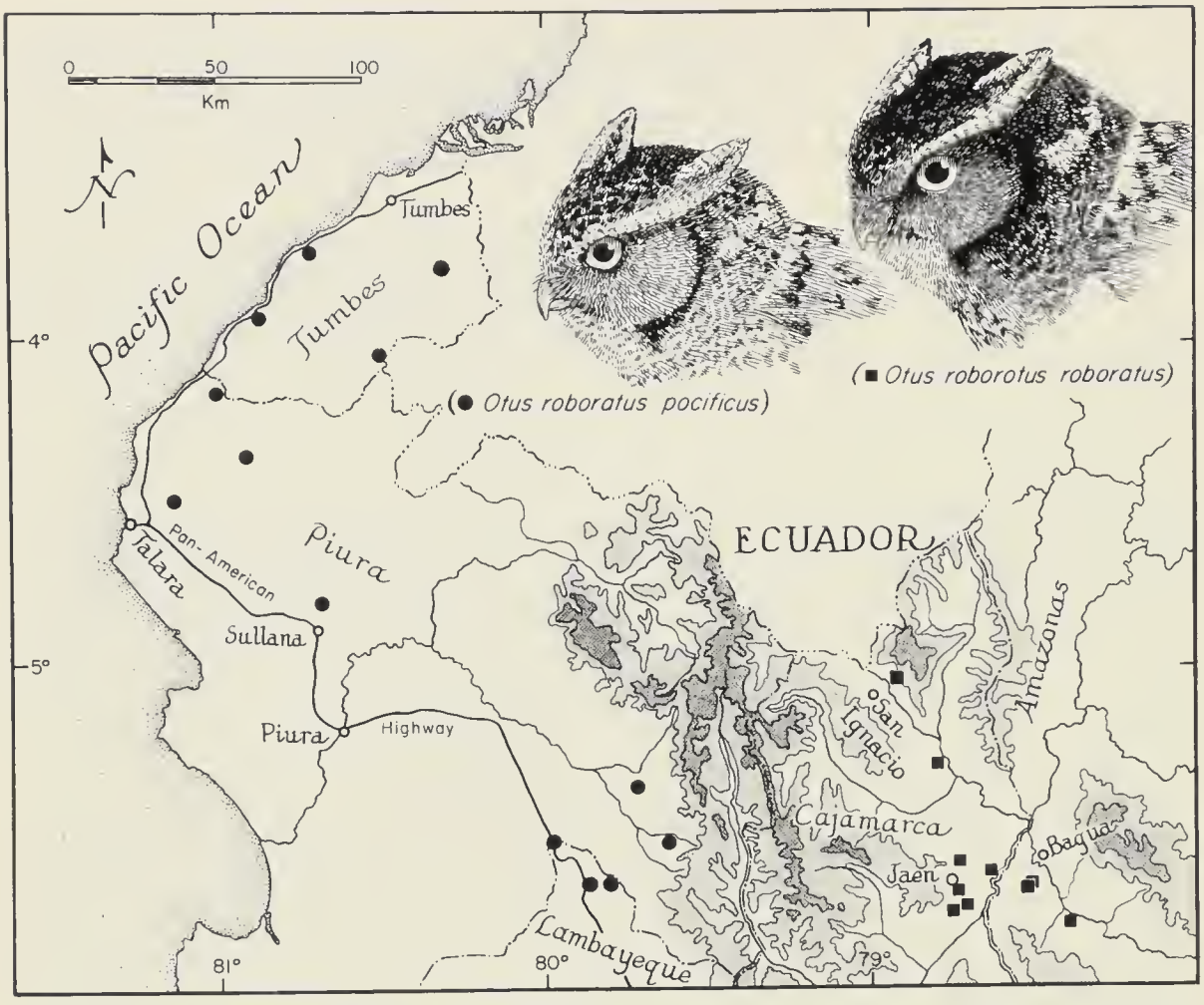

FIG. 1. Localities of occurrence of *Otus roboratus* in northwestern Perú, based on specimens examined in this study. Note that the dots for *O. r. pacificus* all fall west of the western Andes and that all of the squares for *O. r. roboratus* fall in the drainage of the Rio Marañon and Rio Chinchipe, east of the western Andes. The species has been reported beyond the southern boundary of the map (Koepcke 1964:68), but we have not studied specimens from this extra-limital region in order to verify their identity as *O. roboratus*.

resenting either group are very subtle (Fig. 2). As in the desert subspecies of the Western Screech-Owl (*O. kennicottii*) (Miller and Miller 1951:162–163, Marshall 1967), Peruvian Screech-Owls show great individual variability in: (1) the width and intensity of the dark shaft streaks, (2) the density of the horizontal vermiculations or vague "bars" found lateral to the shaft streaks, and (3) the background color, both dorsally and ventrally. In general, shaft streaks are wider and more contrasting in Marañon birds, especially on the upper breast and around the margins of the facial disk (Fig. 2, right). Differences in the lateral vermiculations on the body feathers are extremely subtle. Although there is much overlap, on the average it appears that Marañon specimens are slightly paler than northwestern coastal birds because of reduced lateral vermiculation. Overall

TABLE 1
SUMMARY STATISTICS FOR FOUR SIZE CHARACTERS OF *OTUS ROBORATUS*

Character	Region	Males			Females		
		N	$\bar{x}$	SD	N	$\bar{x}$	SD
Wing length (mm)	Marañon	16	167.6	5.51	8	169.9	4.12
	NW coast	13	140.8	3.48	11	141.7	5.22
Signif. of diff.:[a]	$t_{27} = 15.910$***		$t_{17} = 13.128$***				
Tail length (mm)	Marañon	16	92.3	3.66	8	91.6	1.94
	NW coast	12	76.8	2.63	8	78.6	4.18
Signif. of diff.:	$t_{26} = 13.024$***		$t_{14} = 7.95$***				
Bill length(mm)	Marañon	15	11.9	0.63	8	12.1	0.87
	NW coast	12	10.5	0.51	5	10.2	0.93
Signif. of diff.:	$t_{25} = 6.395$***		$t_{11} = 3.671$**				
Body mass (gm)	Marañon	7	143.9	11.08	3	161.7	2.52
	NW coast	10	86.9	9.41	7	87.7	10.97
Signif. of diff.:	$t_{15} = 11.086$***		$t_{8} = 16.835$***				

[a] One asterisk: $P < 0.05$; two asterisks: $P < 0.01$; three asterisks: $P < 0.001$.

background color is again extremely variable. Nonetheless, differences seem to pertain, with Marañon specimens averaging browner and coastal birds averaging grayer, but with much overlap.

Several specimen tags were annotated with data on the colors of soft parts. A single example from the Marañon Valley had golden-yellow irides with "pinkish-olive" eyelids. The bill of this specimen was grayish-olive with a yellowish tip. The feet were grayish-olive. Nine specimens from northwestern coastal Perú had data on eye color. Six, including one juvenile, had yellow irides, one was noted as having a "golden-yellow" iris, one had a yellow iris with a greenish cast, and one juvenile had a "pale yellow-olive" iris. Bills of the coastal birds were described variously as greenish, dark gray (2), greenish-gray with a yellow-green tip, dark bluish-gray, and "dusty pea green with dusty yellow tip." The feet of coastal specimens were noted as being dark-gray, gray, grayish-flesh, dark greenish-gray, or brownish. The meager information at hand does not indicate any difference in soft part colors between birds representing Marañon versus coastal populations.

Voice.—The primary song of both northwestern coastal and Marañon populations consists of a trill which is approximately 1.5 to 2 seconds in length. This trill is composed of low-pitched repetitive notes that begin softly, peak in loudness, then softly fade (Fig. 3A, B, D, E). The small samples available reveal no differences between birds representing pop-

TABLE 2

SUMMARY STATISTICS FOR SIX COLOR CHARACTERS OF MORPHS OF *OTUS ROBORATUS*

Character	Region	Gray-brown phase			Red phase		
		N	$\bar{x}$	SD	N	$\bar{x}$	SD
Brightness of crown (%)	Marañon	21	4.38	0.73	3	4.27	0.86
	NW coast	11	4.88	0.67	1	6.18	—
Signif. of diff.:[a] $t_{30} = 1.936$ ($P < 0.10$)							
Dominant wavelength of crown (mμ)	Marañon	21	584.4	1.04	3	585.4	1.39
	NW coast	11	582.9	1.70	1	586.4	—
Signif. of diff.: $t_{30} = 2.698$* ($P < 0.02$)							
Purity of crown (%)	Marañon	21	20.43	2.79	3	24.75	3.34
	NW coast	11	23.44	4.67	1	35.69	—
Signif. of diff.: $t_{30} = 1.962$ ($P < 0.10$)							
Brightness of lower dorsum	Marañon	21	6.69	0.89	3	7.16	0.89
	NW coast	11	7.49	0.93	1	6.91	—
Signif. of diff.: $t_{30} = 2.344$*							
Dominant wavelength, lower dorsum	Marañon	21	584.1	0.58	3	586.6	0.65
	NW coast	11	582.6	0.87	1	586.6	—
Signif. of diff.: $t_{30} = 4.969$***							
Purity, lower dorsum	Marañon	21	29.51	3.59	3	37.80	0.96
	NW coast	11	24.27	3.73	1	37.31	—
Signif. of diff.: $t_{30} = 3.832$***							

[a] See Table 1.

ulations on either side of the western Andes. Aggressive barks (Fig. 3C, F) are also similar between coastal and Marañon birds, although samples again are very small. Our recordings and audiospectrograms of *O. roboratus* show clearly that the vocalizations of the Peruvian Screech-Owl are broadly similar to those of other species in the New World group of *Otus* defined by Van der Weyden (1975).

SUBSPECIES

From the aforementioned data on character variation, we conclude that the populations of the Rio Chinchipe drainage and the mid-Marañon Valley and the populations of the lowlands and foothills of northwestern coastal Perú represent different subspecies:

Otus roboratus roboratus

Otus roboratus Bangs and Noble, 1918:448–449.

Type specimens.—Holotype: Adult male, No. 80073, Museum of Com-

parative Zoology, collected September 25, 1916, by G. K. Noble (not examined). Paratype: Adult male, No. 80072, Museum of Comparative Zoology, collected September 14 (17?), 1916, at Perico, Perú by G. K. Noble (examined).

Type locality.—Bellavista, Perú.

Measurements of type.—Wing, 168 mm; tail, 82; tarsus, 39; culmen from cere, 14 (from Bangs and Noble 1918:449).

Geographic range.—Drainages of the Rio Chinchipe and Rio Marañon in the Departments of Amazonas and Cajamarca, northern Perú. Southern limits of range poorly understood (see remarks below).

Characters.—Resembles *O. r. pacificus* of northwestern Perú but averages approximately 28–30 mm longer in wing length, 14–16 mm longer in tail length, 1.5–2.0 mm longer in bill length, and 56–73 gm heavier in body mass. In coloration, *O. r. roboratus* averages browner and has wider and more contrasting shaft streaks on the upper breast and facial disk than does *O. r. pacificus.*

Specimens examined.—24. PERÚ: Depto. Cajamarca.—Perico, Rio Chinchipe, 1 ([MCZ=] Museum of Comparative Zoology, Harvard), 11 ([AMNH=] American Museum of Natural History); below San Jose de Lourdes, 1 ([LSUMZ=] Louisiana State Univ. Museum of Zoology, Baton Rouge); Jaen, 2400 ft., Lower Marañon Valley, 2 (AMNH); 9 km S Jaen, 1 (LSUMZ); 5 mi. SSE Jaen, 3000 ft., 1 ([MVZ=] Museum of Vertebrate Zoology). Depto. Amazonas.—8 km WSW Bagua, 1500 ft., 4 (MVZ); Hda. Caimito, 10 km SE Bagua Grande, 1 (MVZ); 10 km WSW Bagua Chica, 1700 ft., 2 (MVZ).

Remarks.—A specimen (LSUMZ 97573) taken April 29, 1980, on the slopes west of San Damian at 64 road kilometers east of Huarmey, 2100 m, in the Department of Ancash, Perú, seems to represent *O. roboratus* in view of its blackish crown set off by a pale nuchal collar and the general patterning of the plumage otherwise. In size (wing length, 159 mm; tail length, 84.5 mm) it is too large to be *O. r. pacificus.* Instead, the form *O. r. roboratus* is suggested. However, the specimen is grayer dorsally and has wider and bolder ventral shaft streaks than any specimen of the latter form examined. These differences, considered together with the remoteness and elevational displacement of this locality from the known range of *O. r. roboratus,* also indicate that the specimen from Ancash could represent an undescribed subspecies.

Otus roboratus pacificus

Otus guatemalae pacificus Hekstra 1982:58.

Otus guatemalae rufus Hekstra 1982:58–59.

Type specimen.—Holotype: Adult female, No. 1902.3.13.1564 (pub-

FIG. 2. Photographs of male specimens of *Otus* in dorsal (left) and ventral (right) aspect. From left to right: *O. guatemalae guatemalae* (MVZ 142430, Guatemala); *O. roboratus roboratus* (MVZ 160801, Dept. Amazonas, Perú); *O. roboratus pacificus* (MVZ

lished incorrectly as 023.13.1564 by Hekstra [1982:58]), British Museum (Natural History), Tring, collected August 27, 1899, by P. O. Simons (not examined).

Type locality.—Morropon, 140 m, Piura, NW Perú.

Measurements of type.—Wing, 150 mm (from Hekstra 1982:58). Joe T. Marshall, Jr. (pers. comm.) has also measured the type specimen: wing chord, 143; tail, 79. Hekstra presumably measured the flattened wing, hence the discrepancy with Marshall's value for wing chord.

Geographic range.—Coastal lowlands and foothills of northwestern Perú in the Departments of Tumbes, Piura and Lambayeque. Known from a single locality in Ecuador (see below). Both the northern and the southern limits of distribution are uncertain.

163707, Dept. Tumbes, Perú); and *O. choliba crucigerus* (MVZ 120482, Dept. Huila, Colombia).

Characters.—Resembles *O. r. roboratus* of the mid-Marañon drainage east of the western Andes but much smaller in length of wing, length of tail, length of bill and body mass and averaging slightly grayer, especially dorsally.

Specimens examined. 23.—PERÚ. Depto. Tumbes.—Quebrada Faical, 400 m. E El Caucho, 24 km SE Pampa de Hospital, 1 (LSUMZ); Canoas (near Mancora), 1 ([MHNJP] Museo Historia Natural Javier Prado, Lima); Quebrada Bocapan, 50 ft., 6 km S and 4 km W Zorritos, 2 (MVZ); Huasimo, 1 ([FMNH=] Field Museum of Natural History). Depto. Piura.—Parinas, 100 ft., 7 km N and 15 km E Talara, 6 (MVZ); Palambla, "3900–6500 ft.," 1 (AMNH); Amotape Mts., Sullana, 1 (FMNH); Barranco, 11 km N & 28 km E Cabo Blanco, 1 (MVZ); ca 3

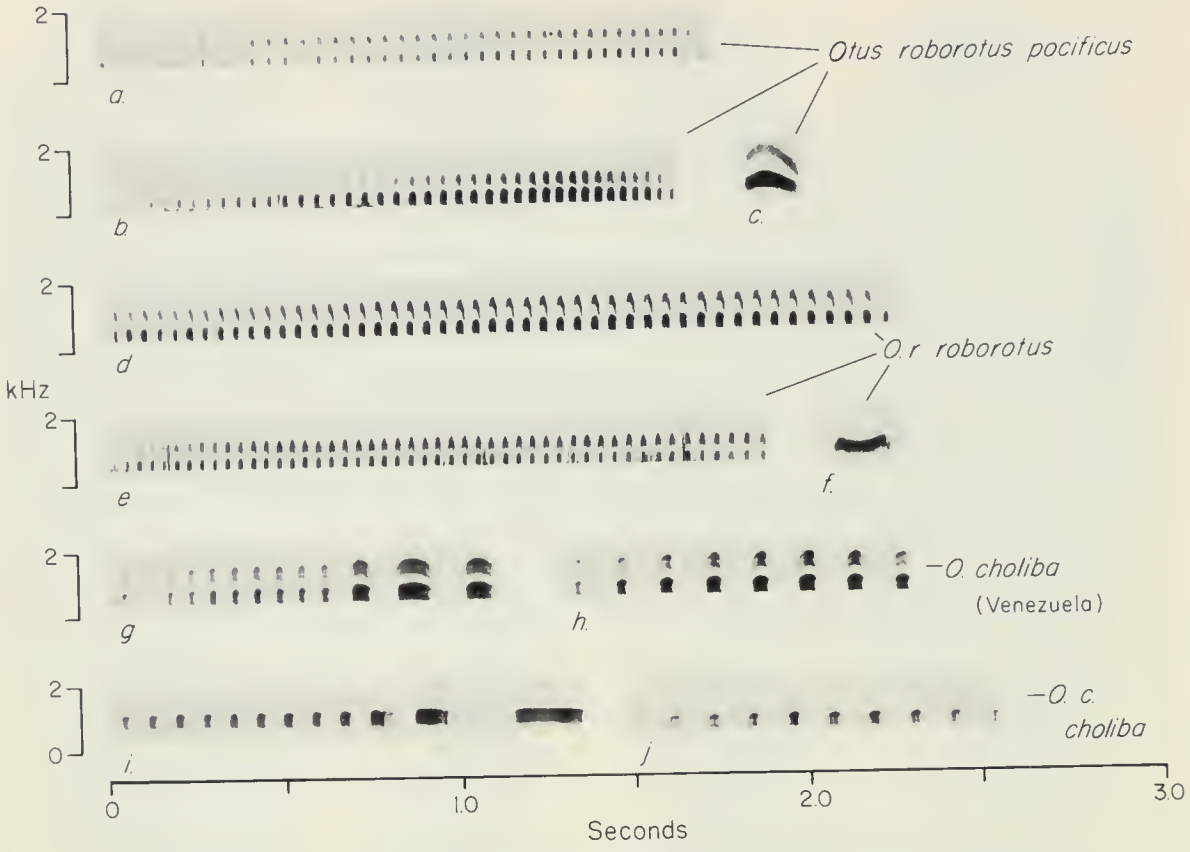

FIG. 3. Audiospectrograms of tape recordings of the common vocalizations of *Otus roboratus* and *Otus choliba*. (a) Advertising song of *O. r. pacificus* (MVZ tape 16, cut 7, cue 11), recorded by the authors at Parinas, 100 feet elevation, 7 km N and 15 km E. Talara, Depto. Piura, Perú, on October 29, 1974. (b) Advertising song of *O. r. pacificus* (MVZ tape 16, cut 8, cue 1), recorded by the authors at Quebrada Bocapan, 50 feet elevation, 6 km S and 4 km W of Zorritos, Depto. Tumbes, Perú, on October 30, 1974. (c) Bark of same male as recorded in b (cue 23). (d) Advertising song of *O. r. roboratus* (MVZ tape 15, cut 3, cue 2) recorded by the authors at 5 miles SSE Jaen, 3000 feet elevation, Depto. Cajamarca, Perú, on August 22, 1970. (e) Advertising song of *O. r. roboratus* (MVZ tape 15, cut 6, cue 26) recorded by the authors at 10 km WSW Bagua Chica, 1700 feet elevation, Depto. Amazonas, Perú, on August 31, 1970. (f) Bark of same individual recorded in e (cue 14). (g) Advertising song with terminal barks of *Otus choliba,* recorded by Paul Schwartz in Venezuela. Subspecies, exact locality, and date unknown. (h) Advertising song lacking terminal barks in *Otus choliba.* Same individual as in g. (i) Advertising song of *Otus choliba choliba* (MVZ tape 94, cut 2, cue 1), with terminal barks. Recorded by Victoria Dziadosz at El Tirol, 230 meters elevation, 19.5 km by road NNE Encarnacion, Depto. Itapua, Paraguay, on September 15, 1978. (j) Advertising song of *Otus choliba choliba* (MVZ tape 94, cut 1) in which the terminal emphatic notes (barks) are lacking. Same recordist, locality, and date as in i.

km by road N Chignia, ca 1000 ft., 1 (LSUMZ); Barbecoas, 500–600 m. cerca de Angolo, Hda. Mallares (cerca Sullana), 1 (MHNJP). Depto. Lambayeque.—Rio Tocto, ca 600 ft., ca 14 km N and 10 km E Olmos, 1 (LSUMZ); Las Pampas, 90 m, km 885, Old Pan-American Highway, 11

km N Olmos, 4 (LSUMZ); 11 road km N Naupe, 275 m, 1 (LSUMZ); 0.5 mi. N Rafan (between Mocupe and Lagunas), 3 m, 1 (LSUMZ).

Additional specimens known.—3. PERÚ. Depto. Piura.—Near Angolo, Hacienda Mallares, near Sullana, 700 m, N Perú coastal district, 1 ([AKMB=] Alexander Koenig Museum, Bonn), fide J. S. Weske, in litt., January 23, 1979. Depto. La Libertad.—Below Hacienda Llaguen (7°40′, 78°40′) fide J. S. Weske, in litt. January 23, 1979, 1 (AKMB). ECUADOR. Balzar Mtns. "Coll. Illingworth, Mar. 1880," 1 (BMNH, Tring No. 88.7.20.64).

Remarks.—Hekstra (1982:58–59) named *Otus guatemalae rufus,* here considered a synonym of *O. r. pacificus,* and chose the specimen from the Balzar Mtns., Ecuador listed immediately above as the type. He incorrectly designated the type as being in the United States National Museum instead of the British Museum (Natural History). Furthermore, in his list of additional specimens examined he mentioned a skin from the Field Museum of Natural History ("ChiNHM 222288" from "NW Peru at Tumbes"). This specimen, actually labelled number 222285 is from Huasimo, Tumbes, as listed above, and represents the red phase of *O. r. pacificus.*

A specimen from Vinces, Ecuador, mentioned by Bangs and Noble (1918:449) and Chapman (1926:246) as possibly belonging to *O. roboratus,* was also included by Hekstra (1982:58) under the name *O. g. rufus.* We have not examined this specimen and therefore cannot comment on its specific identity.

HABITAT AND ECOLOGY

Populations of the Peruvian Screech-Owl inhabit the Arid Tropical Zone (Chapman 1926) where vegetation ranges from open dry scrub comprised of various shrubs, cacti, and scattered short trees to dry deciduous forest composed of various kinds of small to moderately sized trees and columnar cactus (*Cereus*). Species of *Capparis, Acacia, Prosopis,* and *Bombax* are typically represented. Parker et al. (1982:23–24) illustrate these habitats. Most specimens with labels annotated as to habitat were taken in mesquite woodland (=algarrobal) and acacia scrub in washes or on arid hillsides. One individual was found roosting "in center of shrub in desert scrub on slope of foothills." Others were discovered roosting in cavities in mesquite.

The food habits of this species were unknown prior to this study (Hekstra 1973). Specimen tag data on stomach contents show that both subspecies are largely insectivorous, perhaps entirely so. Five stomachs of *O. r. roboratus* contained several different kinds of caterpillars, two large orthopterans, orthopterans, orthopterans and caterpillars, and one grass-

hopper. Fourteen stomachs of *O. r. pacificus* held insect parts (3), insect and grasshopper parts, a cricket and two beetle larvae, six beetle larvae and beetle elytra, 15 caterpillars, 21 2.5 cm (1-inch) long moth caterpillars, seven beetle larvae, beetle larvae, beetles and cricket, beetles and caterpillars. One stomach was full of beetle parts, and one was empty.

INTERSPECIFIC RELATIONSHIPS

The foregoing data on territorial song and plumage pattern establish conspecificity of the northwest coastal populations (*O. r. pacificus*) with those of the Rio Chinchipe drainage and Marañon Valley (*O. r. roboratus*). This conclusion disagrees with the classification of Hekstra (1982), who lacking vocal information, included *pacificus* as a subspecies of *O. guatemalae* and categorized nominate *O. roboratus* as a race of *O. choliba*. Although the songs of *O. guatemalae* and *O. roboratus* are superficially similar (compare Fig. 3 of the present paper with fig. 11 in Marshall [1967: 51] and fig. 2d in Van der Weyden [1975:70]), those of *O. guatemalae* are approximately four times longer (9+ sec) than those of *O. roboratus* (2+ sec). Furthermore, the plumage patterns of *O. guatemalae* and *O. roboratus* are entirely different (Fig. 2).

Alliance of *O. r. roboratus* with *O. choliba* is supported neither by plumage pattern (Fig. 2) nor by voice. The latter species often accents its trill with terminal barks (Fig. 2G–I) which are lacking in either form of *O. roboratus*.

DISCUSSION

Decisions on taxonomic status.—The situation described here, that of disjunct allopatry of taxa which are 100% distinctive in one or more characters, is seen commonly in Neotropical birds. Lacking the test of sympatry of such strong differentiates, we must base taxonomic decisions on indirect criteria. We assume that reproductive isolation in these largely nocturnal birds is achieved mainly by behavioral means, with the advertising song of the male playing an especially significant role. Great similarity or identity of the songs of birds representing both major groups of populations suggest that reproductive isolation probably could not be effected by voice alone in these owls. We are left with body size as the major difference between the two groups of populations. Could body size influence mate choice if sympatry were to occur? Although the answer to this question is unknown, geographic differentiation in the Western Screech-Owl provides some relevant information. In this species, subspecies closely comparable in size to *O. r. roboratus* and *O. r. pacificus* are represented (Miller and Miller 1951). In contrast to the situation in the Peruvian

Screech-Owl, in *O. kennicotti* the large form (*O. k. quercinus*) of the San Diegan district and northern Baja California and the small form (*O. k. xantusi*) of southern Baja are divided by a form intermediate in size (*O. k. cardonensis*) with which both presumably intergrade in northcentral Baja. Thus, the two most divergent forms do not contact directly and, therefore, the examples are not strictly comparable. Nonetheless. the example of *O. kennicottii* at least illustrates subspecific size divergence comparable to that seen in *O. roboratus*. On this basis we speculate that *O. r. roboratus* and *O. r. pacificus* probably would be reproductively compatible, despite their striking size difference and lack of intergradation, and therefore regard them as subspecies. This conclusion would not deny their phylogenetic species status, however, under the criteria of Cracraft (1983).

Conservation.—Within its range and in appropriate habitat, the Peruvian Screech-Owl can be encountered regularly by imitating their trilled vocalizations at night in order to elicit aggressive responses, especially of males. At localities where we have worked, our estimates of their numbers justify the expression "common," or locally, "very common." In view of the comparatively limited geographic distribution of both known forms of the species, however, conservation issues become important despite substantial local numbers. During our work in the early 1970s, the arid woodlands of northern Perú were being seriously impacted by two sources—browsing by goats and destruction by firewood gatherers and charcoal producers. A brief tour of the Olmos region of Lambayeque and the Rio Chinchipe-San Ignacio region of Cajamarca in July 1983 further verified the continued and increased habitat degradation from these sources. One favorable aspect of this owl's ecology is its ability to occupy very sparse woodland and scrub, at least for foraging and, probably to a lesser extent, for roosting, a habit shared by the Western Screech-Owl in the deserts of the southwestern United States (Miller and Miller 1951). However, our limited knowledge of the life history of the species suggests that nesting probably could not occur in such open habitat without trees of at least moderate stature which could provide nesting cavities. Therefore, any useful conservation strategy for the protection of the Peruvian Screech-Owl should at least include the safeguard of senescent trees. Provision of artifical nest boxes should be tried locally where old cavity-bearing trees have been removed. Although destruction of the mesquite woodlands by goat browsing and by firewood gathering will be difficult to control because of the pastoral economy typical of many areas of rural northwestern Perú, charcoal harvesting for barbeques ("asados") should be discouraged or prohibited wherever possible.

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J. W. Fitzpatrick, W. E. Lanyon, R. A. Paynter, Jr., and J. V. Remsen loaned specimens from collections under their care. Our field work in 1970 was funded by grants from the National Geographic Society, the American Philosophical Society and O. P. Pearson, through the Museum of Vertebrate Zoology. The late Carl B. Koford introduced us to Perú and guided us to the sites where owls had been taken. Manuel and Isabel Plenge of Lima provided crucial logistic support and warm hospitality. J. T. Marshall, Jr. sent slides, tape recordings and comments on specimens and classification. Assistance of diverse kinds was provided by S. W. Cardiff, S. Coats, the late E. Eisenmann, L. Jones, the late M. Koepcke, C. Martinez, T. A. Parker III, J. P. O'Neill, J. V. Remsen, and J. W. Weske. To all of the above individuals we extend our sincere thanks.

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VARIATION IN SIZE AND SHAPE IN PIGEONS, *COLUMBA LIVIA*

RICHARD F. JOHNSTON[1]

ABSTRACT.—Morphometric studies of Rock Doves and feral pigeons (*Columba livia*) are enhanced by knowing that variation in size and shape has a well-studied genetic causation in domestic pigeons. Size distributions of skeletal elements of the sexes approximate normality; males are significantly larger than females. Size as measured by principal component I of feral females shows significant interlocality variation, and tends to increase with latitude in North America. Size of males shows no such geographic patterning. Relative limb lengths vary inversely with core size in feral pigeons. Large pigeons have proportionately shorter wings, heavier wing-loading, and are likely to fly faster than small ones. This may explain why homing pigeons tend to be larger than feral pigeons, which are more like wild Rock Doves than homers. Since feral colonies could be colonized by domestics of all sizes, the absence of very small and very large birds probably reflects results of interbreeding of colonizers with resident ferals, and ultimately natural selection for intermediate sizes. *Received 24 April 1989, accepted 26 Aug. 1989.*

Variation in size and shape in Rock Doves[2] (*Columba livia*) is in some ways more interesting to examine than that of many other kinds of birds because humans have been modifying size and shape of domestic and feral pigeons by artificial selection for thousands of generations (Levi 1974, Sossinka 1982). Captive stocks have been genetically modified for a wide range of sizes (Wexelsen 1937); feral populations may be expected to show evidence of this, variably depending on recency of colonization and genetic composition of the early sources, the frequency and genetic composition of current immigrants, the nature of any directional natural selection, and the magnitude of environmental induction of size. Such conditions could well lead to idiosyncratic size variation in feral pigeons in contrast to patterns found in other species (Jackson 1970; Power 1970; James 1970, 1983; Johnston and Selander 1971; Calder 1984).

Information on sizes of feral pigeons has long been generally available (e.g., Olson and Miller 1958, Levi 1974). Additionally, sexual size dimorphism was noted in studies of the genetics of size (e.g., Wexelsen

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[2] This is commonly accepted by North Americans as the vernacular name of wild and feral *C. livia* (but see British Ornithologists' Union Records Committee [1988] for current British usage). Even so, names of domestic and feral derivates of Rock Doves have a long history in English, antedating any codification of vernacular nomenclature, as *pigeon, domestic pigeon, dovecote pigeon,* and *feral pigeon,* among others; wild *C. livia* has always been called Rock Pigeon by some (e.g., Darwin 1868). In this paper the name Rock Dove will be reserved for specimens of wild *C. livia,* and the expressions feral pigeon and domestic pigeon will be used for specimens of feral and domestic sources.

TABLE 1

SCORES ON THE FIRST PRINCIPAL COMPONENT OF VARIATION IN SKELETAL SIZE OF *COLUMBA LIVIA* FROM NORTH AMERICA AND EUROPE

Localities	Principal Component I[a]					
	Males			Females		
	N	Mean	SD	N	Mean	SD
Lawrence, KS	11	4.12	0.53	12	2.70	0.72
Chicago, IL–Madison, WI	16	4.49	0.60	10	3.52	0.54
Edmonton, Alta.	21	4.57	0.56	9	3.94	0.68
Ann Arbor, MI–Pittsburgh, PA	9	4.10	0.76	10	3.54	0.75
Ottawa–Toronto, Ont.	10	4.75	0.75	5	3.51	0.13
New Haven, CT–New York, NY	7	4.10	0.58	17	3.42	0.51
Washington, DC–Gainesville, FL	15	4.27	0.62	9	3.64	0.76
Berkeley, CA	2	4.12	1.07	5	3.13	1.02
North-central Italy	4	3.13	0.83	3	2.53	0.49
Rock Doves	2	3.64	0.88	4	2.51	0.60
Racing Homers	8	6.16	2.50	5	5.38	0.14

[a] Of 16 skeletal variables of size, computed from the ln-transformed data and the covariance matrix of the pooled sexes.

1937) and has been examined at least twice for population samples (Burley 1981a, Johnston and Johnson 1989). Differences in sizes of the sexes have also been documented for Rock Doves in faunal works (e.g., Witherby et al. 1940). Shape of pigeons has been examined in studies of bird flight (e.g., Rayner 1988).

This report examines the size and shape of skeletons of feral pigeons and Rock Doves from a number of localities. Analyses of univariate and multivariate sexual size dimorphism are presented; specific characteristics of locality samples are displayed, along with geographic variation in sexual size dimorphism; and shape differences among pigeons of different sizes are noted.

MATERIALS AND METHODS

Skeletons of pigeons were assembled in the course of field work or through loans from several institutions; adults providing measurements totaled 105 males and 89 females (Table 1). Geographic sources included parts of the Mediterranean Basin and northwestern Europe, Canada, and the United States. Most of the specimens came from feral populations, but six were Rock Doves.

A small set of birds of "homing pigeon" stock ("homers") was separated from several of the locality samples. The birds were identified as homers if they had been fitted with leg bands used by persons who raise and fly homing pigeons. These collectively were treated as a sample in some of the analyses described below, although they came from widely separated sources in both North America and Europe. In this study, homer characters were of large size. Unidentified large individuals might have been homers, might have had recent

TABLE 2

SUMMARY STATISTICS FOR SKELETAL MEASUREMENTS FOR THE SEXES OF *COLUMBA LIVIA*, LOCALITIES POOLED

Character	Males (105)		Females (89)			
	Mean	SD	Mean	SD	F^a	P^b
Premaxilla length	22.3	1.17	21.6	1.27	17.72	<0.002
Premaxilla width	3.0	2.09	2.9	1.77	8.58	0.06
Skull length	33.2	1.20	32.1	1.14	46.87	<0.002
Skull width	19.4	0.59	18.6	0.51	91.51	<0.002
Mandible width	4.5	0.22	4.3	0.22	12.63	0.008
Scapula length	44.7	1.95	42.8	1.85	48.47	<0.002
Coracoid length	34.3	1.39	32.7	1.47	62.68	<0.002
Sternum length	66.0	2.79	63.4	2.79	44.03	<0.002
Sternum depth	35.4	1.67	33.6	1.90	48.27	<0.002
Keel length	70.4	3.27	69.1	3.18	50.88	<0.002
Femur length	39.1	1.70	37.1	1.71	63.69	<0.002
Tibiotarsus length	58.1	2.52	56.0	2.47	32.32	<0.002
Tarsometatarsus length	31.7	1.47	30.2	1.45	51.57	<0.002
Humerus length	45.4	1.78	43.5	1.81	58.02	<0.002
Ulna length	54.9	2.29	52.6	2.19	49.93	<0.002
Carpometacarpus length	33.6	1.84	32.3	1.46	29.50	<0.002

[a] ANOVA *F*-values computed on ln-transformed characters of the total sample.
[b] Bonferroni correction applied.

homer ancestry, or might have been large for other reasons. Four males and eight females fell into the subset of possible homers by discriminant function analysis, but were analyzed as parts of the locality samples in which they were received.

Sixteen bony size variables were measured with dial calipers to 0.01 mm (Table 2); most measurements were obtained as per protocols of Johnston and Selander (1971) or McGillivray (1985), but mandible width was taken as the least distance across the articular surface.

Computations were done on an IBM 3081 KX3 mainframe computer using BMDP (Dixon 1988) or on a hand calculator. Size over the 16 variables was summarized by principal component analyses (PCA; BMDP4M). For assessment of size generally and within each sex, the data for both sexes were pooled, ln-transformed and the covariance matrix employed; use of both sexes generates large size variance and thus produces a common size component (PC-I), with shape being partialled over subsequent axes (Hamilton and Johnston 1978, Somers 1986). For PCA comparisons of shape the raw data were handled through the correlation matrix. PC scores vary around a mean of zero, so in order to enhance comparison of individuals 4 was added to each score, making them all positive.

Descriptive statistics were computed using BMDP2D. Geographic variation in size was assessed through one-way analysis of variance (ANOVA, BMDP7D) and discriminant function analysis (BMDP7M). Possible interaction between sexual size dimorphism (SSD) and interlocality size variation was examined by two-way ANOVA. Differences between means were examined by *t*-tests (BMDP3D) or ANOVA *F*s. Regressions were performed by means of BMDP2R. Degree of SSD for individual characters is presented either in the form of

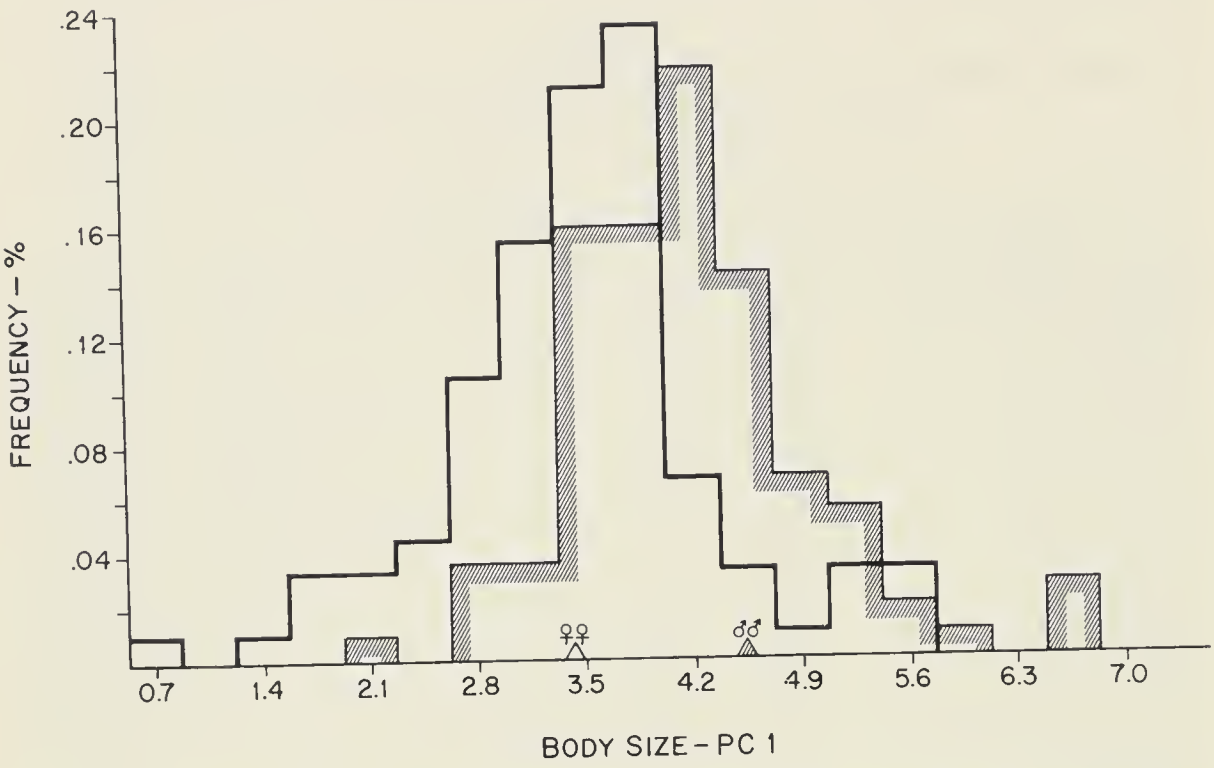

FIG. 1. Frequency distribution of sizes of 194 specimens of females (left histogram) and males (right histogram) of *Columba livia*. The principal component I scores for individuals were obtained from a PCA over 16 variables of skeletal size using ln-transformed data and the variance-covariance matrix for the pooled sexes. An ANOVA of the two samples provided $F = 64.26$ (df = 1, 192, $P = 0.0001$), describing highly significant size dimorphism.

F-values from an ANOVA or of the dimorphism index (DI) of Storer (1966). The DI is calculated as a percentage of the means for each sex ($100(\bar{X}m - \bar{x}f)/(\bar{x}f + \bar{x}m)/2$), in which $\bar{x}f$ and $\bar{x}m$ symbolize means of females and males.

RESULTS

Variation in size.—The distribution of sizes of adult males and females using scores of individuals on PC-I is shown in Table 1 and Fig. 1. Considerable sexual size overlap is displayed, and males are larger than females. The distribution of the entire sample (not shown) is normal (Shapiro and Wilk's [1965] W = 0.99, $P = 0.69$); that for the females is likewise normal (W = 0.98, $P = 0.61$), but that for the males is skewed to the right (W = 0.95, $P = 0.005$); the latter finding reflects the comparatively few small individuals relative to the numbers of large individuals in the sample of males.

Univariate SSD is given in Table 2; differences in sizes of the sexes for any one of the variables run around 2 to 4 percent. Interlocality variation also occurs, but does not statistically interact with SSD (Table 3, for North American specimens). Males are larger than females in all but two vari-

TABLE 3

SEXUAL SIZE DIMORPHISM AND INTERLOCALITY VARIATION IN SIZE OF CHARACTERS OF THE SKELETON OF NORTH AMERICAN *COLUMBA LIVIA*[a]

Character	*F*-Value		
	Sexual dimorphism	Localities	Interaction of SD and loc.
Premaxilla length	13.79**	1.42	0.33
Premaxilla width	5.78	5.31**	0.92
Skull length	38.84**	4.50**	0.65
Skull width	54.09**	3.10*	0.66
Mandible width	7.34*	2.82*	0.81
Scapula length	24.14	0.66	0.73
Coracoid length	33.92*	0.72	0.46
Sternum length	36.22**	1.20	1.21
Sternum depth	25.11*	1.14	0.28
Keel length	41.53**	2.28	1.61
Femur length	49.59**	3.06*	0.99
Tibiotarsus length	19.73**	3.68*	1.36
Tarsometatarsus length	25.90**	3.65*	0.63
Humerus length	44.15**	2.22	1.33
Ulna length	36.69**	2.86*	1.07
Carpometacarpus length	18.69**	2.52	1.01
PC-I	58.38**	3.66*	1.24

[a] The ln-transformed data for 91 males and 77 females from 8 localities were analyzed in a two-way ANOVA (BMDP 7D; Dixon 1988) in which sex and locality were the independent variables. Statistical significance: * = <0.05, ** = <0.01 (Bonferroni correction applied).

ables of skeletal size as well as PC-I; 9 of the 17 show significant interlocality variation.

Although no interaction between SSD and geographic variation is found in Table 3, the dimorphism index for localities computed on PC-I varies widely but without pattern. Some interplay between sex and locality, or sex and size, is noted in a comparison of SSD in different samples (Table 4). A consistent and high-level SSD, similar to that in the overall specimen set, is found in the sample from eastern Kansas. Specimens from Alberta, Canada, and the heterogeneous set of homers, however, show a lesser degree of dimorphism. Only for male homers, among which one specimen is exceptionally small (for a homer, that is; it is still larger than 85% of all specimens), are inflated variances noted for any variable. The patterning of dimorphism of the 16 variables in the sample from Edmonton and the homers is similar; correlating the rank-ordered variables in degree of dimorphism from large to small across the two samples produces a coefficient of $r_s = 0.47$ (N = 16; $P < 0.05$). The specimens of the two

TABLE 4

COMPARISON OF SEXUAL SIZE DIMORPHISM OF VARIABLES IN THREE SAMPLES OF SKELETONS OF *COLUMBA LIVIA*

Variable	Dimorphism index[a]		
	Homers	Alberta	Kansas
Premaxilla length	0.9	1.0	1.7
Premaxilla width	4.3	1.9	1.9
Skull length	0.9	0.3	1.4*
Skull width	1.7	0.7	1.7**
Mandible width	2.1	2.0	2.8
Scapula length	0.8	0.5	1.6**
Coracoid length	0.9	0.6	2.0**
Sternum length	0.5	0.5	1.4**
Sternum depth	0.7	0.8	2.0*
Keel length	1.0	0.5	1.7**
Femur length	1.0	0.8	1.9**
Tibiotarsus length	0.4	0.5	1.5**
Tarsometatarsus length	0.8	1.2	1.8**
Humerus length	1.0	0.8	1.6**
Ulna length	0.8	0.8	1.8**
Carpometacarpus length	1.2	0.9	1.7**

[a] Indexes were calculated on means of the ln-transformed male and female data for each locality; significance of the differences between means was tested by T and is indicated by the following levels: * = <0.05, ** = <0.01 (Bonferroni correction applied).

samples are not only similar in reduced size dimorphism, but also in the degree to which each variable shows dimorphism.

Patterning of interlocality size variation is weak in the present samples. North American males from 8 localities show significant variation for only 5 of the 16 individual variables. North American females from 9 localities, however, show significant variation in PC-I scores and in 13 of the 16 individual variables. A regression of scores of females on PC-I with latitude for 9 North American localities was marginally significant ($r = 0.66$; $F = 5.33$; df = 1, 7, $P = 0.06$).

Variation in shape.—Lengths of limb elements vary inversely with central-core sizes in this sample. Most of the correlations are not statistically significant, but the patterning is clear: the six limb elements (as well as the coracoid and scapula) have negative correlations on PC-II, and the body core elements, (along with those of the skull) have positive correlations (Table 5). Scores on PC-II failed to regress on latitude in either sex. The scores also showed no sexual dimorphism (ANOVA $F = 0.81$; df = 1, 192, $P > 0.37$).

The change in relative limb lengths with "size" is usually described as

TABLE 5

CORRELATIONS[a] OF THE ORIGINAL VARIABLES WITH PRINCIPAL COMPONENTS I AND II FROM MATRICES OF SIZE CHARACTERS OF SKELETONS OF *COLUMBA LIVIA*

Variable	Females (89)		Males (105)	
	PC I	PC II	PC I	PC II
Premaxilla length	0.612	0.114	0.738	0.079
Premaxilla width	0.489	**0.544**	0.493	**0.560**
Skull length	0.777	0.087	0.800	0.153
Skull width	0.611	0.063	0.560	**0.378**
Mandible width	0.566	**0.370**	0.780	**0.332**
Scapula length	0.899	−0.006	0.866	−0.058
Coracoid length	0.929	−0.175	0.915	−0.220
Sternum length	0.884	0.186	0.857	0.231
Sternum depth	0.760	**0.411**	0.781	0.006
Keel length	0.843	0.209	0.843	**0.281**
Femur length	0.743	**−0.292**	0.901	−0.168
Tibiotarsus length	0.919	**−0.267**	0.902	−0.212
Tarsometatarsus length	0.902	−0.163	0.890	−0.158
Humerus length	0.935	−0.208	0.925	−0.245
Ulna length	0.950	−0.197	0.929	**−0.275**
Carpometacarpus length	0.921	−0.158	0.821	−0.180
Eigenvalue	10.484	1.026	10.807	1.048
% of Variance	0.66	0.06	0.68	0.06

[a] Computed from raw data and the correlation matrices. Correlation for PC-II larger than ±2.66 (♀♀) or ±2.53 (♂♂) are significant at the 0.01 level, and are printed in bold-face type.

allometric. As noted before, body size in feral pigeons is satisfactorily summarized by PC-I. If wing bone elements of individuals are plotted against their PC-I scores, a strongly linear relationship is evident (Fig. 2, for humerus length). PC-I evidently increases more rapidly than length of humerus, because ratios of humerus length to PC-I are smaller for large than for small individuals.

DISCUSSION

Size.—Classical assessment of size in Rock Doves of Europe and North Africa shows variation to be clinal, small to the south and larger to the north (review in Cramp 1985). Variation in size of feral pigeons is less predictable than in wild birds, and only that of North American females varies in accordance with accepted ecogeographic theory (James 1970, Murphy 1985). Given that North American ferals have had in excess of 400 generations in which to adjust to environmental pressures acting on variation in size, the lack of size patterns might indicate a slow response to selection. The conclusion probably is unwarranted, however, in part

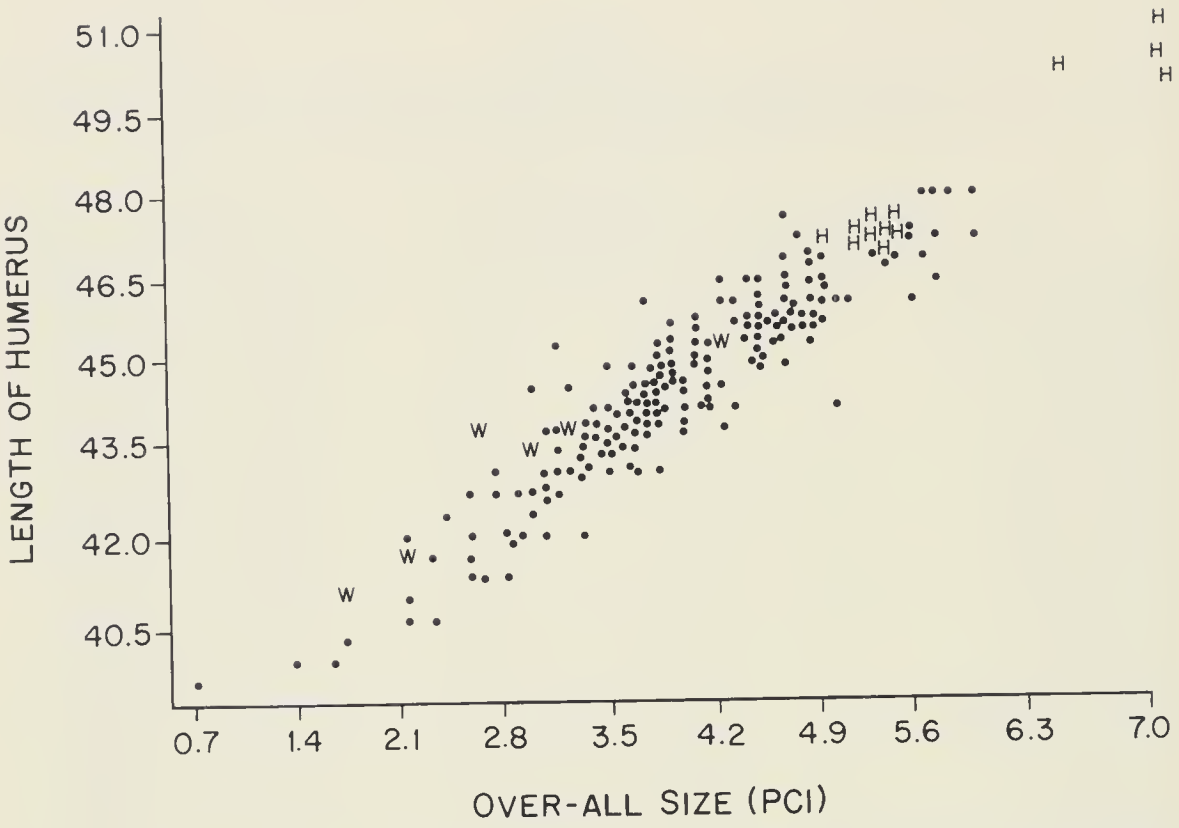

FIG. 2. Length of humerus as a function of over-all size for 194 specimens of *Columba livia* from North America and Europe. The dots represent feral pigeons from the USA, Canada, and Italy; the W's represent Rock Doves from the Mediterranean Basin; the H's represent homing pigeons from northern Italy and several North American localities. The correlation is $r_p = 0.94$; $P = 0.001$.

because genes from domestic stock are still entering feral gene pools. It is impossible to know the number of such immigrants, but racing homers regularly join feral colonies. Size of the ancestors of ferals (i.e., domestics) has long been under artificial selection by humans (Levi 1974), so it is inevitable that intrusions of domestics into feral colonies introduce otherwise uncharacteristic variation in size into feral populations.

Even if rates of immigration of domestics to feral colonies are unknown, some nontrivial deductions about size of ferals can be made. For example, if ferals from Edmonton are significantly larger than those from Kansas, this is likely to be genetically based because the birds at Edmonton are large in the same aspects of the skeleton as homers, and artificial selection is responsible for the large size of homers. Notable also is the reduction, when compared to populations of smaller birds, of number of elements showing significant SSD and the degree of SSD in each of the elements in both the Edmonton sample and the homers. Again, this may reflect selection, though of different sorts, in both samples. It is parsimonious

to assume that the similarities in size and SSD between birds from Edmonton and homers are owing to similar causes, as is examined beyond.

This is not the same as saying that the birds at Edmonton are likely to have been derived from homers, although that is a possibility. It is more likely that the Edmonton birds have the same ancestry as the rest of North American ferals—a variety of domestic sources—so that their present approach to size and shape of homers is a consequence of natural selection for large size or covariates thereof. The earliest records of the introduction of domestic pigeons in North America actually are for Canada (1606, in Nova Scotia; Schorger 1952). Adjustments to high latitude North American environments by feral pigeons have therefore been occurring for perhaps 470 generations (figuring a generation at 9 months; Johnston and Johnson 1990), which, despite probably continual immigration of domestics throughout that time, should have been enough to allow natural selection to modify size.

Clearly, racing homers are a problem in such considerations because they are likely to be the most consistent domestic immigrants into feral colonies; their history is therefore of some consequence. Modern homers were developed in the late 19th and early 20th centuries by crosses among several domestic varieties of pigeon, including the smerle, cumulet, dragoon, horseman, and English carrier (Levi 1974). All these are (or were—the cumulet, dragoon, and horseman are extinct) known as muscular and/or deep-keeled birds, and the dragoon, horseman, and carrier were large.

Homers are not the largest variety of domestic pigeon (e.g., Riddle et al. 1932), and presently seem to be only indirectly selected for large size. Levi (1974) writes that one selects for a blocky body build with deep keel, hard or durable plumage, and for speed of return on homing flights. Selecting for speed of return should indirectly select for large size, because rapid flight is necessitated by high wing-loading (Rayner 1988). Wing-loading varies allometrically with body mass, because wing area varies as the square of linear dimensions, whereas body mass varies as the cube. If the relatively large size of homers is partly an allometric result of selecting for high speed of flight, a relatively simple genetic basis could be involved—breeders selecting for flight speed would actually be working on allelic frequencies at a few genetic size loci amenable to artificial selection.

If, as here conjectured, the feral birds in Canadian populations are large owing to selection, they will have achieved body size-wing loading characteristics of homers not artificially but as a consequence of natural selection. Thus, if the high-latitude Canadian populations have been selected for large body size, they will have recapitulated for North America the clinal size pattern found in European Rock Doves.

This wing length-body size allometry is implied in the bivariate relationship between length of humerus and body size as quantified by PC-I (Fig. 2). Most specimens occur in the mid-range of the two axes, at or slightly above the locations of the wild specimens. Homers plot in the upper right of the graph and are joined by 20 of the largest birds in various samples, of which a third come from Edmonton. All these individuals have shorter humeri relative to body size than do Rock Doves or most ferals. My argument necessarily assumes that shorter wing bones relative to body size increases wing-loading.

Sexual size dimorphism.—The present samples of feral pigeons suggest that degree of SSD is geographically localized, but that variation in SSD has no interlocality pattern. Should the pattern of size variation shown by the female samples—increasing size on latitude—be supported by larger samples, then we may find SSD to decrease with latitude. Based on present samples, SSD of feral pigeons appears to decrease either with latitudinal increase or with body size increase. If the latter, the decrease in SSD could be a consequence of allometry; if only the former, the decrease would be difficult to interpret, and could involve unlikely scenarios such as relaxation of sexual selection.

Sexual shape dimorphism.—Lack of sexual dimorphism on PC-II, the component representing variation in shape, conforms to the null hypothesis. This means that variation in the shapes of pigeons from large to small is the same for both sexes—the allometric relationships are evident in males and females alike. This is necessary to demonstrate in the data set, because no theoretical basis for the sexes of pigeons having different allometries has ever been advanced.

Conclusions.—Within the limits of these samples, it appears that the variation in size of feral birds is similar to that of Rock Doves. Since it is unlikely that very large and very small domestic pigeons are differentially prevented from escaping to feral populations, their absence from the samples must stem from causes other than capability of escape. Possible scenarios include the following:

(1) Under the assumptions that some very large or small birds living in feral colonies are of high or adequate fitness and that most other individuals are of average size, the large or small birds will probably mate with, respectively, smaller or larger ferals. They would thus tend to leave offspring of intermediate sizes. In support of the first assumption, large individuals are known (Burley 1981b, Johnston and Johnson 1989) to be preferred mates, and large individuals of both sexes probably have high reproductive fitness (Johnston and Johnson 1990). In support of the second, crosses between pigeon varieties of different sizes inevitably produce offspring of intermediate sizes (Wexelsen 1937). There is, how-

ever, no satisfactory demonstration of above average fitness for small pigeons under feral conditions.

(2) Under an assumption that some very large or small birds in feral colonies are of low fitness, they may not survive to time of reproduction, they may not be able to form a pairbond if they survive, or they may be inadequate parents if they manage to pair. In support of the assumption, small individuals are least preferred at the time of mate choice (Burley 1981b) and they evidently compete poorly with larger pigeons for food (Murton et al. 1972). Very large size may be disadvantageous under conditions of food scarcity, owing to absolutely high maintenance costs and leading to inadequate nutrition of the individual or its offspring (cf Ricklefs 1974). Large individuals of heavy wing-loading fly under metabolically costly conditions (Pennycuick 1968, Rayner 1988), leading them to make heavier demands on food resources than smaller birds (Norberg 1981).

Accordingly, it appears likely that feral pigeon populations are subjected to stabilizing selection on body size. Only in colonies regularly infiltrated by racing homers would distribution of body sizes be positively skewed, as is found in Ontario, Canada.

Sexual dimorphism in size occurs along conventional lines except for the suggestion that SSD may decrease on latitude. Sexual dimorphism in shape is unlikely to be found in *C. livia.*

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HAWK MOUNTAIN-ZEISS RAPTOR RESEARCH AWARD

The HAWK MOUNTAIN SANCTUARY ASSOCIATION jointly awarded the 1990 Hawk Mountain-Zeiss Raptor Research Award to Eduardo E. Iñigo Elias at the University of Florida and Karen L. Wiebe at the University of Saskatchewan. Iñigo's project is entitled "Effects of forest fragmentation on a tropical raptor community in the biosphere reserve of "Montes Azules" in the Lacandona region of Chiapas, Mexico" and Wiebe is studying "The effect of food supply on reproductive decisions and success in the American Kestrel."

The Hawk Mountain Sanctuary Association is now accepting applications for its fourteenth annual award to support student research on birds of prey. Support for this award is provided by Carl Zeiss Optical, Inc. Up to $2000 in funds are available and will be awarded to one or two recipients. To apply, a student applicant should submit a brief description of his or her research program (five pages maximum), a *curriculum vitae,* a budget summary including other funding anticipated, and two letters of recommendation to Dr. James C. Bednarz, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529, USA. The deadline for applications is 15 November 1990. The Association's board of directors will make a final decision in February 1991. Only undergraduate and graduate students in degree-granting institutions are eligible to apply. The awards will be granted on the basis of the project's potential to improve understanding of raptor biology and its ultimate relevance to the conservation of raptor populations. Applications from anywhere in the world will be considered.

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PLUMAGE AND BEHAVIORAL DEVELOPMENT OF NESTLING WHITE IBISES

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Abstract.—We describe the physical characteristics and behavioral development of 17 hand-reared and more than 400 parent-reared nestling White Ibises (*Eudocimus albus*) hatched in 1985 through 1988 at Pumpkinseed Island, a large colony site in coastal South Carolina. Hatchling ibises are covered with a Pale Neutral Gray to Jet Black natal plumage. About 30% of the hatchlings possess a tuft of white feathers on their crown, and this pattern persists throughout the nestling period. Juvenal plumage, which is complete by 60 days, is mainly Vandyke Brown and Blackish Neutral Gray dorsally and creamy white ventrally. The bill, which is straight at hatching, begins to curve downward at about 14 days. Nestling White Ibises exhibit considerable individual variation in bill markings from approximately 10 days of age through fledging. Increasingly persistent begging vocalizations begin within hours of hatching. Nestlings walk on partially extended legs at eight days of age, pirate food from other nestlings and form creches at 21 days of age, and fledge and join all juvenile and mixed-age feeding flocks at 45–55 days of age. We suggest that the phenotypic variability in plumage, bill coloration, and begging calls we describe enables parental ibises to identify more easily their offspring at the colony site. *Received 27 Feb. 1989, accepted 12 Nov. 1989.*

Although the plumage and behavioral development of several species of wading birds has been studied in considerable detail (e.g., Hammerkops [*Scopus umbretta*], Wilson et al. 1988; storks, Kahl 1962, 1966; Thomas 1984; herons, Gross 1923; Gavino and Dickerman 1972; Juarez and Dickerman 1972; Mc Vaugh 1972, 1975; Snow 1974; Merritt 1981), there are few detailed studies of juvenile ibises. Michelmore and Oliver (1982) describe the plumage and behavioral development of 10 hand-reared and a number of parent-reared Northern Bald Ibises (*Geronticus eremita*) raised at the Jersey Wildlife Preservation Trust. Rudegeair (1975) describes interactions between free-ranging nestling White Ibises (*Eudocimus albus*) and their parents at a colony site in north central Florida. Kushlan provides information on the behavior of free-ranging White Ibises in south Florida (Kushlan 1974), as well as information on growth of body parts of five hand-reared birds (Kushlan 1977a). Beebe (1914) provides a description of changes in behavior, as well as in plumage and soft body parts, of two parent-reared White Ibises maintained at the Bronx

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Zoo and a number of nestlings raised by free-ranging adults in the wild. He also noted variation in bill markings in young ibises. ffrench and Haverschmidt (1970) outline changes in the plumage and soft parts of developing nestling Scarlet Ibises (*E. ruber*), noting that some nestlings have a "white tuft on the crown." Luthin (1983) compares the appearances of nestling Bare-faced (*Phimosus infuscatus*), Green (*Mesembrinibis cayennensis*), and Scarlet ibises.

White Ibises typically breed in large colonies. Colonies vary considerably in size, but ibises usually nest in the company of at least 10 pairs of conspecifics, and many colony sites exceed several thousand pairs (Kushlan 1977b). Nestling ibises are ambulatory at about eight days of age, and they spend several weeks in large creches at breeding colonies being fed by adult ibises before becoming independent at six to seven weeks of age (Rudegeair 1975). Studies of other colonial species where the young intermingle reveal considerable phenotypic variability in nestling plumage and voice, presumably in response to selection for parental recognition of offspring (cf. Buckley and Buckley 1970, Berry 1975, Stoddard and Beecher 1983). Here we: (1) detail extensive observations of 17 hand-reared captive White Ibises together with incidental observations of more than 400 parent-reared nestlings, (2) compare development in White Ibises with that of other species of wading birds, and (3) discuss our observations of phenotypic variability among nestlings in terms of selection for parental recognition.

MATERIALS AND METHODS

Seventeen 8- to 72-h-old newly hatched White Ibises were taken from a large breeding colony on Pumpkinseed Island in Winyah Bay, Georgetown County, South Carolina, in July 1986 (eight young from eight nests) and 1987 (nine young from six nests). (See Frederick 1987 for a description of the colony site.) Chicks were individually marked with colored pipe cleaner leg bands and transported to rearing facilities at the Savannah River Ecology Laboratory near Aiken, South Carolina. Initially, chicks were maintained in small (14.5 × 24 × 6 cm) plastic baskets lined with crumpled paper. Two of these small baskets, containing two or three chicks each, were placed in larger baskets (60 × 45 × 40 cm). Infrared lamps were used to maintain an ambient temperature of approximately 30°C, and insect netting was draped over the larger baskets each evening to protect nestlings from mosquitos. When chicks became ambulatory at about two weeks of age, they were transferred to a 3 × 4 × 2.5 m indoor-outdoor aviary equipped with branches, plastic boxes for roosting, and a wading pool. Chicks were moved to the indoor portion of the enclosure each evening, where a heat lamp maintained the temperature at approximately 25°C. When they were approximately six weeks of age, the birds were placed in a 9.5 × 14.5 × 4.8 m outdoor flight aviary equipped with flow-through wading pools and natural vegetation.

During the first 35 days, the birds were fed a ground mixture of 65% beef heart, 24% hard-boiled egg, and 11% crayfish (Cambaridae) and fish, fortified with calcium carbonate (0.88%), dicalcium phosphate (0.41%), vitamin premix (0.25%), trace minerals (0.05%), and selenium premix (0.005%) (See Bolden and Jensen 1985). Water was added to the mixture

to create a slurry for feeding. Young chicks were stimulated to gape by applying light pressure on the gonys with the base of the index and middle fingers. We then poured the food slurry into the mouths of the chicks using a narrow spoon. During the first week, chicks were fed every 2 h from 07:00 h to 21:00 h. Beginning on Day 8, chicks were fed every 2 h from 09:00 to 19:00 h. On Day 15, we stopped feeding the chicks the diet in slurry form and began offering the same dietary components cut into 1.3-cm cubes five times a day at 3-h intervals. At this age we began to encourage the chicks to feed independently by "pecking" at food items with the index finger; however, most of the food was still being fed by hand. Throughout the period of hand feeding, birds were fed only until intense begging had ceased, and care was taken not to overfeed the chicks (cf. Archibald et al. 1980). Beginning on Day 22, chicks were provided with food in a feeding tray four times a day at 3-h intervals. At the same time, a commercially prepared diet consisting of horse meat, horse-meat by-products, corn, soy, barley, fish meal, eggs, yeast, and a vitamin and mineral supplement (Bird of Prey Diet, Central Nebraska Packing Inc., North Platte, Nebraska) was gradually introduced in place of the beef heart. Birds were fed twice daily during the sixth week. At 12 weeks of age, the birds were gradually switched to a diet of 67% Bird of Prey Diet, 17% fish or shrimp meal, and 17% dog meal. Water was provided ad libitum once the chicks were ambulatory.

Birds were weighed on a triple-beam balance to the nearest 0.5 g on alternate days through six weeks of age, and then twice monthly until they reached asymptotic mass. Changes in plumage and behavior were recorded daily until the birds were six weeks old. Color descriptions of plumage and hard and soft body parts were made according to Smithe (1975), except where noted. In 1986, we photographed each bird at least once a week throughout the study period. Facial patterns and coloration of the 1987 nestlings were documented with photographs taken when the chicks were 24–31 days old. We recorded the begging calls of the nine chicks raised in 1987 on a cassette tape recorder between Days 9 and 36. Begging calls were analyzed using a Kay Elemetrics Corp. Sona-Graph.

Observations of more than 400 parent-reared nestlings were made at the colony site in 1985, 1986, 1987, and 1988 during regular visits to the colony to measure developing young, band fledglings, and collect regurgitant samples. We attached backpack radio telemetry units weighing 16–22 g (approximately 3% of their body mass at the time of attachment) to eight 25–31-day-old juveniles (two birds in 1987 and six birds in 1988) to determine when fledglings begin to leave the colony site to forage on their own.

RESULTS

All 17 hand-reared chicks readily accepted the prepared diet and became accustomed to hand feeding. All eight chicks reared in 1986 survived; however, in 1987, two chicks were euthanized (one on Day 17 and one on Day 34) after they developed slipped leg tendons despite the precautions we took to prevent this condition (cf. Archibald et al. 1980). These two chicks appeared healthy in all other respects, and data collected on them prior to the onset of this condition are included below.

Physical Development

Bill and face.—Newly hatched White Ibises have a straight, Flesh Colored (Smithe Color 5) bill, with a Dark Neutral Gray (Color 83) tip. A white egg tooth, which is sloughed at 5–9 days, is located on the distal tip of the upper mandible. The skin surrounding the eyes and on the face is bare, loose-fitting, and Flesh Colored.

This coloration of the bill and face persists for three days. Afterwards, the facial skin and orbital area darken to Light Neutral Gray (Color 85), except in some individuals where a narrow Salmon Color (Color 6) band persists at the base of the upper mandible. The color change proceeds distally until the upper third of both mandibles is Dark Neutral Gray. The remaining portions of the bill change to Salmon Color.

A faint, Light Neutral Gray band appears on the upper mandible immediately distal to the nares between 7 and 10 days. This band gradually becomes Dark Neutral Gray and encircles both upper and lower mandibles by the end of the second week. Gradual downward curving of the bill begins at Day 14. Dark Neutral Gray areas on the proximal, central, and distal portions of the bill gradually increase in size until most of the bill is dark by the beginning of Week 5 (Fig. 1). The pied-bill, which persists at least through Day 24, varies considerably in pattern, even among chicks of the same age (Fig. 2). The dark areas of the bill are glossy in some chicks and dull in others. By six weeks the entire bill is Light Neutral Gray. Over the next three weeks, the base of the bill and the orbital area become Pale Pinkish Buff (Color 121 D), while the remainder of the bill becomes Salmon Color.

Legs and feet.—The legs, feet, and nails of newly hatched chicks are Flesh Colored. The nails and legs change to Neutral Gray between 2 and 7 days of age, followed by a darkening of the feet between 4 and 9 days. The coloration of the nails, legs, and feet gradually becomes Medium Neutral Gray (Color 84) or Dark Neutral Gray by Day 11. By the fifth month, the feet and legs change to one of four shades of gray or grayish brown (Pale Neutral Gray [Color 86], Glaucous [Color 80], Light Neutral Gray, or Light Drab [Color 119 C]).

Body skin.—The skin of hatchlings, which is Light Flesh Color, becomes Light Neutral Gray around Day 2 and bluish gray (nearly Plumbeous [Color 78]) by Day 3. By Day 35, the skin is Deep Vinaceous (Color 4).

Eyes.—The eyes begin to open 1–3 days after hatching and are completely open and alert by Day 9. The irises are Raw Umber (Color 223) through the first month. At five months, the outer ring of the iris changes to Medium Plumbeous (Color 87), while the inner portion becomes Pratt's Payne's Gray (Color 88).

Plumage.—The heads and necks of hatchlings are covered with dense, shiny Jet Black (Color 89) down which, on the crown, projects caudally. Several white feathers form a spot on the crown of approximately 31% of the hatchlings (31.4% of 162 nestlings in 1987, 30.2% of 262 nestlings in 1988). The size of this crown spot, which is randomly distributed among nestlings (Table 1), ranges from 1 to 5 mm in diameter. The remainder of the body is sparsely covered with Pale Neutral Gray down on the underparts and rump, and Dark Neutral Gray down on the shoulders and

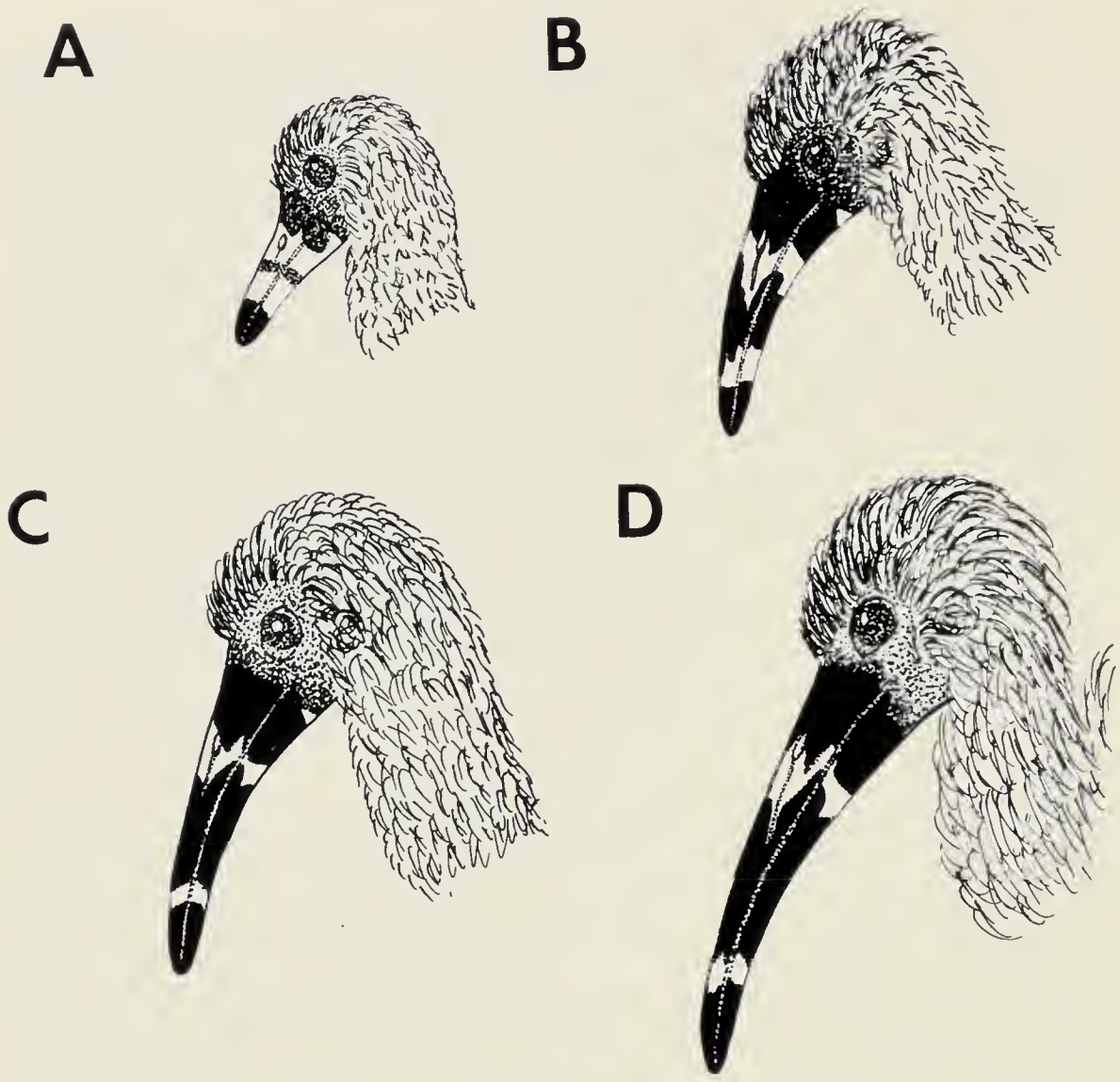

FIG. 1. Bill and facial markings at 7(A), 15(B), 26(C), and 32(D) days-of-age of a single juvenile White Ibis hand-reared in 1986.

wings. For a detailed description of the structure of down feathers of nestling White Ibises see Beebe (1914).

There is no visible feather growth until Day 4 or 5, when primaries begin to emerge. Feathers in the humeral and alular tracts, as well as secondaries and tertiaries, appear between 6 and 10 days. The spinal tract,

→

FIG. 2. Bill and facial markings of four 27–31-day-old, hand-reared White Ibises taken from four different nests in July 1987, along with two begging calls recorded on separate days when the birds were between 23 and 30 days old. Note the similarity in calls within individuals compared with differences among individuals . Horizontal marks on the ordinal axis represent 1 and 5 kHz.

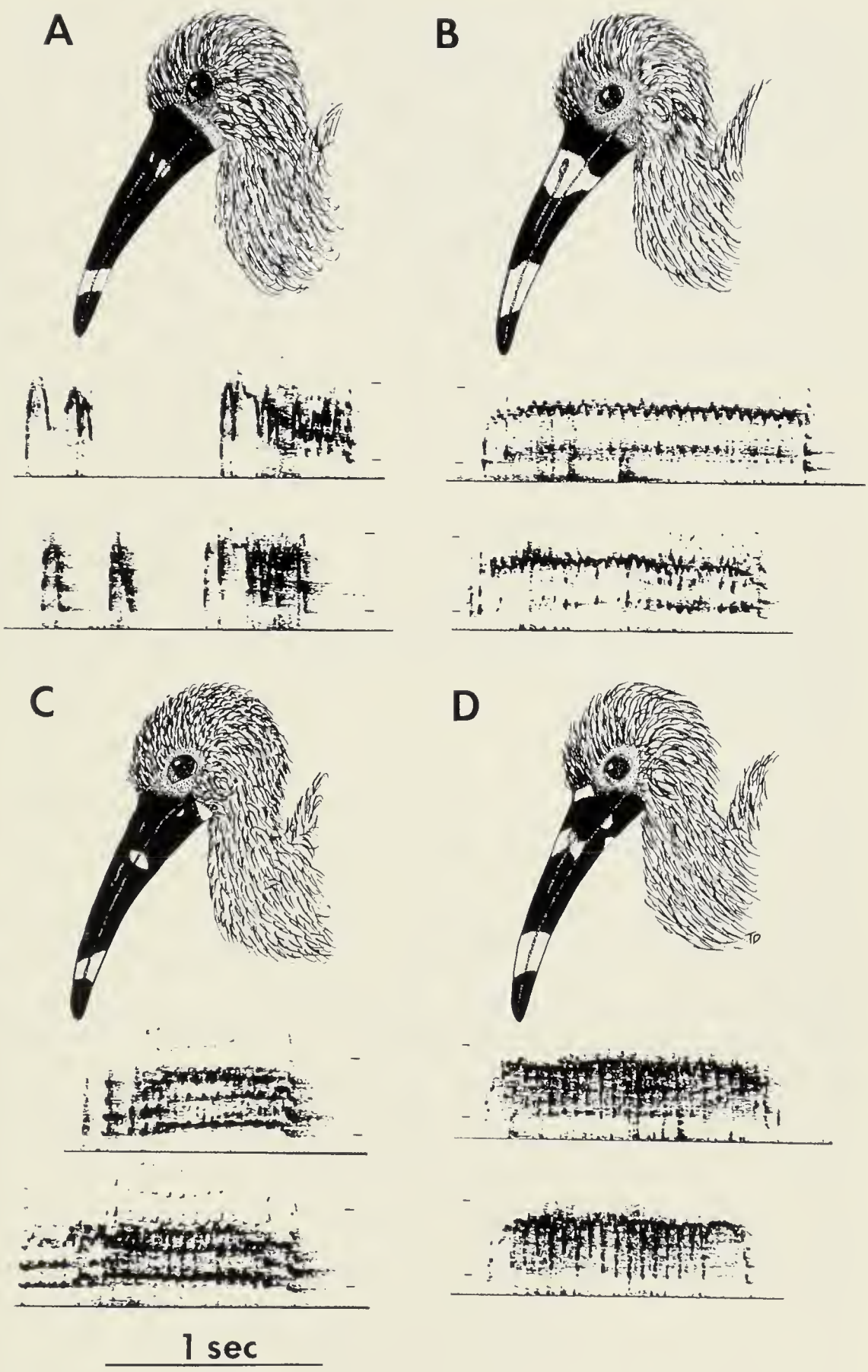
A
B
C
D
1 sec

TABLE 1

DISTRIBUTION OF JUVENILE WHITE IBISES WITH AND WITHOUT WHITE FEATHERS ON THEIR CROWN AMONG 201 NESTS AT THE PUMPKINSEED ISLAND COLONY SITE IN 1987 AND 1988

	Nestlings with white spots : nestlings without white spots	Observed	Expected[a]	P[b]
One-nestling nests (34)[c]	Nestling with spot	10	10.4	
	Nestling without spot	24	23.6	>0.10
Two-nestling nests (108)	0:2	57	52.0	
	1:1	39	45.9	
	2:0	12	10.1	>0.10
Three-nestling nests (55)	0:3	22	18.4	
	1:2	18	24.3	
	2:1	11	10.7	
	3:0	4	1.6	>0.10
Four-nestling nests (3)	0:4	1	0.7	
	1:3	0	1.2	
	2:2	0	0.8	
	3:1	1	0.2	
	4:0	1	0.03	NT[d]

[a] Assuming a random distribution of nestlings with and without spots among all nests. (Because there was no indication of a difference between years in the relative frequencies of nestlings with and without spots [χ^2 test for heterogeneity, $\chi^2 = 0.071$, $P > 0.90$], we pooled data from the two years to increase our sample sizes for this analysis.)

[b] Chi-square tests for goodness-of-fit.

[c] Number of nests.

[d] No test because of small sample size.

ventral tract, and rectrices emerge between 8 and 12 days. The crural and femoral tracts emerge between 24 and 32 days. The down on the head is replaced by juvenal plumage between 32 and 46 days.

Unsheathing of feathers generally begins 1–2 days after the shafts emerge. Primaries are completely unsheathed by 45 to 60 days, and the juvenal plumage is nearly complete and smooth by the end of the second month. Feather shafts of the developing juvenal plumage are Plumbeous, changing to creamy white (no description in Smithe 1975). Feathers of the shoulders and wings are Blackish Neutral Gray (Color 82). Feathers of the underparts of the trunk, back, legs, rump, and one third of the base of the rectrices and primaries are creamy white. Feathers of the head and neck are Vandyke Brown (Color 121), with narrow (on the head) or broad (on the neck) lacings of creamy white, giving an overall appearance of Glaucous. By three months, the feathers of the shoulders and wings have faded to Vandyke Brown.

Behavioral Development

Week one captive birds.—The period of the most pronounced developmental change occurs during the first week. Newly hatched chicks,

whose eyes are partially or completely closed, are weak and uncoordinated, and they spend most of their time sleeping in a prone position. On Day 1, begging consists of jerky, lateral head movements and soft trilling vocalizations. At this age, begging can be sustained for only about 3 sec at a time. On Day 2, the chicks can support their heads by balancing them on the base on their necks. At this time, begging movements are more controlled, and the wings are held from the body and moved back and forth horizontally, while the chick trills loudly. On Day 3, chicks can hold their necks off the ground by balancing them on their chests and wrist joints. Trilling is louder than on Day 2. At this time, chicks begin to shuffle backwards to the edge of the "nest" to defecate, a behavior that then persists throughout the nestling period.

By Day 4, chicks support their bodies by sitting on retracted legs, and they are able to stand on their tarsometatarsi for up to 10 sec. At this time, chicks, which beg while resting on their tarsometatarsi and moving their wings vertically with their heads and necks fully extended, forcibly probe their bills into the keeper's hand during feedings. Each begging vocalization lasts for about 2 sec. By Day 6, chicks can stand on extended legs for 15 sec and can crawl on their tarsometatarsi.

Week one free-living birds.—The development of locomotion and vocalizations in free-ranging birds are comparable to those observed in captive-reared birds, with a noticeable progression from tentative, uncoordinated begging in newly hatched chicks to the controlled, sustained begging of 7-day-old chicks. Free-living chicks beg continually unless they are being brooded, even when neither parent is near the nest. Although they are capable of crawling by the end of this period, undisturbed chicks remain in the nest.

Week two captive birds.—Chicks begin walking on their partially extended tarsometatarsi by Day 8, and by Day 14 they are walking on fully extended legs, exploring the area within several meters of the nest, and preening their developing juvenal plumage. Chicks continue to beg through this period while resting on their tarsometatarsi. During the second week, chicks begin to flap one or both wings when begging. At this time, chicks beg for food from other chicks by placing their bill around the closed bill of another chick, moving their head laterally, flapping one wing, and trilling loudly. Solicited chicks were not seen disgorging food.

Week two free-living birds.—In the wild, chicks younger than 15-days-old rarely leave the nest except to flee from approaching humans. When approached by a human, nestlings climb from their elevated nests (7–50 cm off the ground in black needle rush [*Juncus roemerianus*], giant cord grass [*Spartina cynosuroides*], and marsh elder [*Iva futescens*]) into the surrounding vegetation. Chicks are less vocal at this age, and they appear to beg only when a parent is near.

Week three captive birds.—At three weeks, chicks beg and feed more persistently, and they pirate food from each other by jabbing their closed bills through the open bill of a nestling being fed by the keeper. If the harassed nestling drops its food, the food is quickly consumed by the other chicks. At this age, chicks beg by rapidly approaching the keeper while flapping their wings and trilling loudly, and they retreat to a corner of the pen after being fed.

Week three free-living birds.—Chicks spend little time in their nests after they reach 15 days-of-age. Creches of up to at least 30 similar-aged juveniles walk and stand within 20 m of their nests. Food piracy occurs regularly. When solicited, unattended wild chicks disgorge food to both juvenile and adult pirates.

Weeks four and five captive birds.—Chicks now eat from feeding trays most of the time but still solicit food from the keepers. By Week 4, chicks no longer allow the keepers to use their fingers to stimulate gaping, and they accept food without encouragement. At this time, chicks accept less food by hand from the keepers, and body mass stabilizes for 6–10 days until the chicks begin to feed on their own (Fig. 3). Chicks sometimes appear lethargic and subdued during this period. Chicks begin to take short hopping flights between branches, and by the end of Week 5, most birds are able to fly at least 2 m. Chicks increase the number of visits to wading pools, and they begin to exhibit considerable probing behavior.

Weeks four and five free-living birds.—Wild birds spend much time perched on black needle rush and marsh elder, and they take short flights of up to 2 m. They also begin to wade and probe in the shallow water (<10 cm) surrounding the island colony site. Chicks are fed by adults away from their nests while perched on vegetation.

Weeks six and seven.—Captive birds were released a into large flight aviary at this time and continued to beg for food from the keepers. Sustained flights of at least 50 m occurred in free-living ibises at approximately 35–40 days. Young ibises are often seen flying after adults, begging for food. At 45 to 55 days of age, juveniles first leave the island colony site and fly over water for at least 750 m to forage in juvenile or mixed-age flocks of up to 300 individuals. (Eight radio-telemetered chicks left the Pumpkinseed Island colony site between approximately 47 and 56 days of age.)

DISCUSSION

Plumage and behavior appeared to develop in the same manner and at the same rate in hand-reared and parent-reared nestlings, although in our study hand-reared birds achieved the same mass several days later than did parent-reared birds (see also Kushlan 1977c). Even so, several

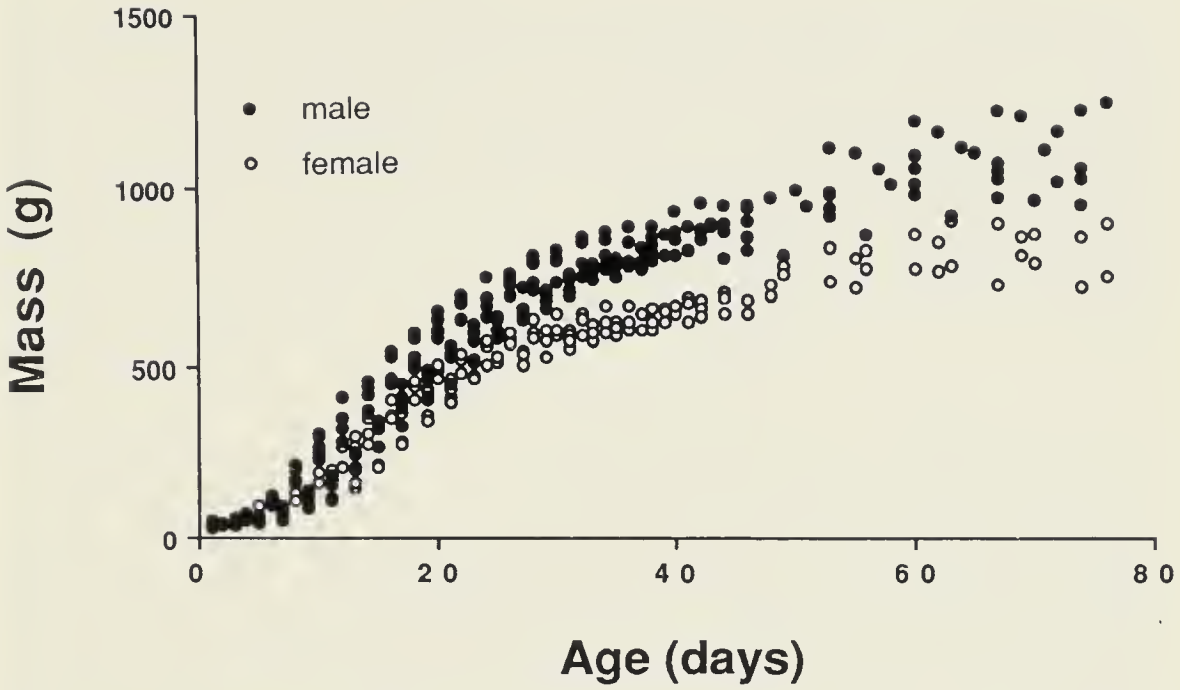

FIG. 3. Body masses of 17 White Ibises hand-reared during 1986 and 1987.

behavioral patterns developed in our hand-reared birds earlier than in parent-reared birds, probably because we tracked the development of hand-reared birds more closely than that of parent-reared birds (cf. Kahl 1966). Overall, there was no indication that the captive birds failed to develop normally (cf. Rudegeair 1975).

The patterns of behavioral and plumage development in nestling White Ibises appear to be nearly identical to that described for the somewhat larger Northern Bald Ibis, although nestling White Ibises develop considerably more rapidly and fledge earlier than do nestling bald ibises (Michelmore and Oliver 1982).

The classic work on White Ibis nestling ontogeny was by Beebe (1914). Overall, our results agree with his earlier report, as well as those of Kushlan (1974, 1977c), Rudegeair (1975), and ffrench and Haverschmidt (1970). Because we tracked changes with age in the appearance of the bills of individual nestlings, we are able to document that the "good deal of variation" in bill patterns first reported by Beebe (1914) is due not only to differences within individuals as they develop, but also to differences among individuals of the same age. Kushlan (1977a, c) reported that hand-reared nestlings increased their mass more slowly than did parent-reared birds, a phenomenon we also noted, even though in our study we found no difference between these two groups with regard to plumage or behavioral development. The reason for the difference in growth is unclear. Kushlan (1977c) suggested that the growth of his captive birds may have

been "similar to that in the wild under stressful conditions." Because our nestlings were part of a long-term study of among-year variance in the growth of nestling ibises and because we wished to reduce within-year variance in our data set, parent-reared birds measured during the course of our study included only first-hatched chicks (De Santo, Johnston, and Bildstein, unpubl. data). Our hand-reared nestlings, however, included both first- and later-hatched individuals, and it may be that part of the difference in the growth rates of these two groups reflects that situation.

Our results demonstrate that White Ibises are ambulatory several weeks before they begin to fly. This developmental sequence parallels Kushlan's (1977a) findings that in young ibises "structures associated with terrestrial locomotion" grow more rapidly than those "associated with flight."

As in many species of wading birds (for examples see Gross 1923; Kahl 1962; Mc Vaugh 1972, 1975; Gaviño and Dickerman 1972; Luthin 1983; Thomas 1984), bill coloration and markings in nestling White Ibises differ considerably from those found in adults. Furthermore, even though the color and pattern of each ibis nestling's bill changes continuously as the bird develops (Fig. 1), by the end of their second week same-aged nestling White Ibises also exhibit considerable individual variation in these characteristics (Fig. 2). The same appears to be true in at least several other species of colonial nesting wading birds (Little Blue Heron [*Egretta caerulea*], Tri-colored Heron [*E. tricolor*], Mc Vaugh 1972; Least Bittern [*Ixobrychus exilis*], Snowy Egret [*E. thula*], Yellow-crowned Night-Heron [*Nyticorax violaceus*], Mc Vaugh 1975; Green-backed Heron [*Butorides striatus*], Gaviño and Dickerman 1972).

Several researchers have suggested that such individual variation, especially in species where individuals nest close to one another or where creching occurs, helps parents recognize their young (Buckley and Buckley 1970, Skutch 1979, O'Connor 1984, Stoddard and Beecher 1983). Individual variation in the bill markings of the White Ibises we reared was obvious by Day 9 (Fig. 2), just prior to the onset of increased mobility and creche formation in the wild. The white crown that occurred on 31% of the nestlings (Table 1) was obvious by Day 2 and remained so throughout the nestling period. ffrench and Haverschmidt (1970) also report the presence of white crown feathers on some of the nestling Scarlet Ibises they studied. We were able to use these markings alone to recognize our captive birds individually. We propose that this extreme variation in the appearances of nestling White Ibises, together with individual variation in the begging calls of nestlings (Fig. 2), function as highly variable "signature traits" (sensu Stoddard and Beecher 1983) that enable parent ibises to locate and preferentially care for their young in large creches.

Stoddard and Beecher (1983) offer data suggesting that, in swallows,

coloniality selects for conspicuous signature traits similar to those we have described for White Ibises. Incidental observations of Glossy Ibises (*Plegadis falcinellus*), which also nest colonially on Pumpkinseed Island, and whose nestlings often creche, suggest considerable individual variation in the head and facial plumage of nestlings (pers. obs., see also Cramp and Simmons 1977). The extent to which nestlings of other species of colonial and, especially, solitary nesting ibises (e.g., Green Ibises) exhibit individual variation is unknown (cf Luthin 1983).

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RECENT POPULATION TRENDS OF THE EASTERN BLUEBIRD

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ABSTRACT.—North American Breeding Bird Survey data for the period 1966–1987 indicate that Eastern Bluebird (*Sialia sialis*) populations declined during the 1970s, primarily in association with either severe winters or severe spring storms. In recent years, bluebird populations have increased to levels similar to those observed during the first year (1966) of the survey. Survey results suggest that climate has an important role in affecting short-term population declines in bluebirds. *Received 20 April 1989, accepted 27 Aug. 1989.*

The population status of the Eastern Bluebird (*Sialia sialis*) has been the subject of considerable public concern. Zeleny (1977) indicated that "During the past forty years, the population . . . may have plummeted by as much as 90 percent" and attributed the decline to competition with House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*) for nest sites, to a decline in winter food supply, human-caused decreases in nest cavities, severe winter weather, and use of pesticides (Zeleny 1976, 1977). Without long-term survey data from breeding areas, it is difficult to assess the relative importance of these environmental influences on changes in bluebird populations.

Even with survey data, however, it is difficult to evaluate the effects of long-term, gradual influences (such as decreases in winter food supply, regional changes in pesticide use, or increased nest box availability) on regional bird populations, as these factors cannot be manipulated experimentally over time and space. Correlational studies must be used to associate these factors with bird population trends, and cause and effect relationships can only be implied. Studies in which environmental factors can be experimentally manipulated are necessary to document accurately the effects of these factors on bird populations (Morrison 1986).

Climatic effects on bird population sizes can be both gradual (occurring over a period of years) or severe. Effects of gradual changes in climate may be difficult to document (see above). Population changes associated with severe weather, however, can be evaluated using data from large-scale geographic surveys. Extreme weather events, such as hurricanes or cold winters, can produce measurable between-year effects on bird populations (Robbins et al. 1986). Documenting declines after periods of severe weather and subsequent population recoveries can provide insight

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into the importance of weather in influencing both the population dynamics of individual species and the structuring of communities (e.g., Wiens 1977).

Severe weather in winter and spring has been associated with declines in Eastern Bluebirds (e.g., Bent 1964). James (1962) analyzed Audubon Christmas count data and found long-term declines in wintering bluebird populations from the mid-1940s until 1961. He documented a strong correlation between cold winters and subsequent declines in Eastern Bluebird populations. However, bird distribution in winter can vary in association with climatic severity, and regional shifts in distribution can influence yearly Christmas count data. Examination of populations during the breeding season provide more accurate representations of population trends over time. Unfortunately, no breeding population survey existed in North America prior to 1966.

We now have 22 years of data from the North American Breeding Bird Survey (BBS, Robbins et al. 1986), which can be used to examine recent population changes in the Eastern Bluebirds. An earlier analysis of the BBS (Robbins et al. 1986) indicated widespread Eastern Bluebird population declines during the period 1966–1978. Extreme local (Pinkowski 1979) and regional (Pitts 1981) declines were noted in association with severe weather during the winter of 1976–1977. In this paper we document the recovery of the population during the period 1978–1987 and suggest that climatic events have been a dominant force in affecting the population trends of Eastern Bluebirds over the period 1966–1987.

METHODS

The North American Breeding Bird Survey.—The BBS is run cooperatively by the United States Fish and Wildlife Service and the Canadian Wildlife Service. Over 2000 randomly located permanent routes are monitored each year in the United States and Canada along approximately 80,000 km of secondary roads. In the eastern part of the continent, the survey was initiated in 1966; however, in the central United States and Canada most routes were begun in 1967. Each BBS route is 39.2 km (24.5 mi) long. An observer drives along the route, stops each 0.8 km (0.5 mi) and observes birds for 3 min. All birds seen or heard at a stop are recorded by species, and the number of birds of each species recorded over the 50 stops is totaled. From these route totals, we estimate population trends and annual indices of abundance. To estimate population trends, we use linear regression of year on the natural logarithm of the route counts (plus 0.5, to eliminate the possibility of a logarithm of 0). We also include observer covariables to account for differences in the ability of observers to perceive birds. Trend is defined as the slope of the year variable back-transformed (Geissler 1984) to provide an estimate of rate of change per year.

Trends for state/provinces, physiographic strata, and other regions are found by first estimating trends by physiographic strata within states. Individual route trends are weighted by average density on a route and the variance of the slope estimate to find these state/stratum estimates. These estimates are then weighted by the number of routes in the state/strata and the areas of state/strata to find regional trends. Variances of the regional trends

are found by bootstrapping, a procedure involving repeated subsampling from the route trends from which regional subestimates are found (Efron 1982). Variances are then estimated from these regional subestimates, and the median of these subestimates is used as the regional trend estimate. We present trends as percent change/year. Statistical significance is assessed using z-tests (Table 1). This trend estimation procedure is similar to that discussed in Robbins et al. (1986, Appendix E), although they did not include observer covariables in their route regressions.

Estimation of annual indices of abundance.—Because the BBS is a route survey, we cannot simply average each year's counts to provide annual indices of abundance. These average counts are biased by missing route data and changes in observers (Geissler and Noon 1981). Instead, we estimate annual indices of abundance for a region by fitting a linear regression to data from each route in which the regional trend estimate has already been incorporated. The residuals from this regression represent the difference between the actual data and the predicted values given the estimated regional trend. These residuals are averaged by year over all routes in the region. They are then added to the regional predicted trend line (which is found by multiplying [to predict forward] or dividing [to predict backward] a regional mean density estimate by the regional trend estimate). Therefore, these residual indices represent the average distance from actual route data to values predicted by the regional trend estimate, adjusted for observer differences, and they provide a measure of goodness of fit of the trend line to the route data.

Eastern Bluebird population trends.—We estimated population trends for the Eastern Bluebird for three time periods: the entire BBS survey period (1966–1987), an early period (1966–1978), and a later period (1978–1987). Trends were estimated for states/provinces, physiographic strata, U.S. Fish and Wildlife Service Regions (see Table 2 for the component states), the United States, Canada, and North America (the entire survey area). Physiographic strata used in the analysis (Droege and Sauer 1989) are slightly revised versions of those presented in Robbins et al. (1986). Annual indices were estimated for states/provinces and other regions for the entire survey period of 1966–1987. We present population trend values for states/provinces, because humans tend to think in terms of political boundaries. The U.S. Fish and Wildlife Service Regions group the states into convenient north–south and east–west groups which summarize regional patterns. Strata results are presented in figures so as to clarify regional patterns in trends.

Relative density contour maps were made using program SURFER (Golden Software, Inc. 1987). Maps were made for two periods, the period of lowest relative abundance (1977–1979) and the most recent three years (1985–1987). For each period, total counts were averaged by route and mathematically interpolated using a Kriging procedure to form density contours (Ripley 1981).

RESULTS

Early years.—The map of population trends by physiographic strata illustrate that the Eastern Bluebird declined throughout most of its range during the early period (Fig. 1). Only one physiographic stratum (the Southern Piedmont region) showed significant increases, and the Prairie regions and Appalachian portions of the midwestern United States contained significant declines in Eastern Bluebird populations. This pattern is reflected in state/provincial trends, in which 18 of the 38 state/provinces showed significant declines ($P < 0.05$), and only one state (North Carolina) had an increasing population (Table 1). All FWS Regions showed signif-

TABLE 1

POPULATION TRENDS (% CHANGE/YEAR) FOR THE EASTERN BLUEBIRD BY STATE/PROVINCE FOR THREE TIME PERIODS

State	1966–87 trends			1966–78 trends			1978–87 trends		
	%	P[a]	N[b]	%	P	N	%	P	N
ALA	2.596	*	50	−4.796	*	40	8.108	**	48
ARK	−0.609		27	−2.935		26	3.667		27
CON	−7.114		15	−9.655		15	1.525		13
DEL	0.729		6	−2.072		6	23.506	**	6
FLA	−6.390	**	33	−6.958	**	31	−5.053		26
GA	2.798		58	−3.468		47	4.843	**	55
ILL	−2.073		54	−19.277	**	49	20.912	**	49
IND	−0.344		36	−16.928	**	16	11.493	**	35
IA	1.187		29	−9.490	**	25	6.870	**	25
KAN	−2.357		30	−10.253	**	30	19.943	**	26
KY	−2.936	**	44	−11.654	**	41	15.948	**	38
LA	36.897		20	0.441		17	27.503	**	14
ME	−2.817		20	−13.717		13	11.099		13
MD	3.388	*	55	−0.757		47	10.004	**	48
MAS	−3.323		13	−6.601	**	13	5.366	*	7
MIC	−6.886	**	62	−10.597	**	44	10.149		44
MIN	3.331		37	−2.485		28	16.638	**	27
MIS	3.885	*	26	1.114		22	6.475	*	23
MO	−0.487		40	−13.027	**	36	15.554	**	36
NEB	4.040		18	0.242		14	11.102		12
NH	6.780		22	2.909		21	10.692		14
NJ	0.826		13	−7.362		9	13.989		7
NY	0.155		101	−4.252	**	85	7.943	**	65
NC	7.278	**	30	5.120	**	24	7.654	*	25
ND	0.006		11	0.062		7	2.749		6
OHi	−3.867	**	43	−9.509	**	38	20.036	**	39
OKL	−1.899		32	−8.722	**	30	8.878	**	29
ONT	−2.445		42	−11.918	**	29	11.957	*	28
PA	1.809		94	0.155		75	6.546	*	64
QUE	7.773	*	11	15.668		9	11.768		7
SC	9.809	**	21	5.876		18	6.173	**	18
SD	−3.822		15	−7.709	**	10	0.193		6
TEN	−1.923	*	44	−4.027	**	42	15.277	**	42
TEX	7.313	**	64	−0.869		52	9.794	**	55
VT	−2.549	**	20	−0.184		18	−6.882		10
VA	6.131	**	46	4.667		38	11.073	**	42
WVA	−2.825		37	−10.655	**	32	5.578		30
WIS	−3.053	**	67	−6.766	**	66	19.803	**	52

[a] Statistical significance of a *z*-test.
[b] N indicates number of routes in the state/province.
* $P < 0.05$; ** $P < 0.01$.

TABLE 2

POPULATION TRENDS (% CHANGE/YEAR) FOR THE EASTERN BLUEBIRD BY REGIONS FOR THREE TIME PERIODS, WITH ASSOCIATED SAMPLE SIZES (N) AND STATISTICAL SIGNIFICANCES

Region	1966–87 trends			1966–78 trends			1978–87 trends		
	%	*P*	N	%	*P*	N	%	*P*	N
FWS Region 2 (TX, OK, MN, AZ)	1.957		99	−5.296	**	84	6.842	**	87
FWS Region 3 (MN, WI, IA, MO, IL, IN, OH)	−1.667	*	368	−11.083	**	302	15.966	**	307
FWS Region 4 (AR, LA, KY, TN, MS, AL, GA, SC, NC, FL)	0.038		353	−5.005	**	308	8.681	**	316
FWS Region 5 (ME, NH, VA, NY, MA, RI, CT, PA, DE, NJ, MD, VA, WV)	1.392		442	−4.885	*	372	8.931	**	319
FWS Region 6 (MT, ND, SD, WY, NE, KS, CO, UT)	−1.934		76	−9.128	**	61	18.108	**	50
Canada	0.524		58	−1.072		42	11.895	**	35
United States	0.119		1338	−6.549	**	1127	9.571	**	1079
North America	0.115		1396	−6.524	**	1169	9.581	**	1114

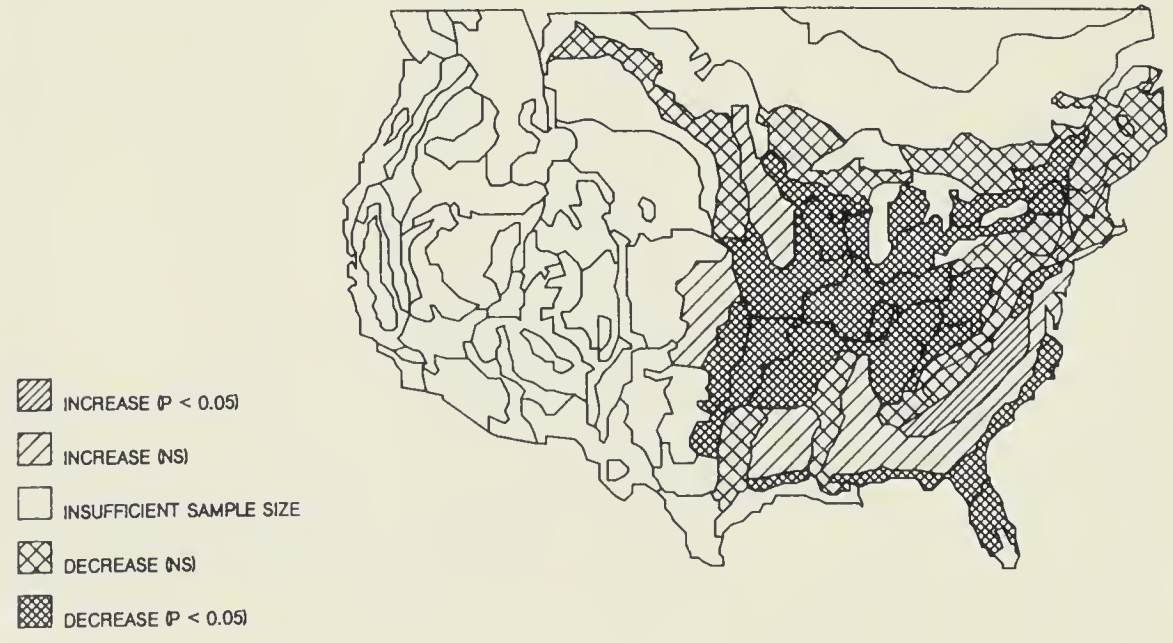
* $P < 0.05$; ** $P < 0.01$.

EASTERN BLUEBIRD

BBS 10 YEAR TREND 1978–87

EASTERN BLUEBIRD

BBS 13 YEAR TREND 1966–78



icant declines, as did the United States and the continent (Table 2). Canada showed a nonsignificant decline.

Late years.—Conversely, almost all physiographic strata had increasing Eastern Bluebird populations during 1978–1987 (Fig. 1). Similarly, 25 states had significantly increasing populations, and no states showed a significant decline (Table 1). All regions analyzed also had significant increases in Eastern Bluebird populations (Table 2).

Entire survey period.—Survey results reflect the patterns of the two subperiods, with the southern United States showing increasing populations of Eastern Bluebirds and more northerly strata showing generally a mosaic of nonsignificant increases and declines, except for several significantly declining populations in the Appalachian foothills (Fig. 2). State trends also reflect this variable pattern, with seven states showing significant declines and seven states showing significant increases (Table 1). Only FWS Region 3 shows a significant decline, and all other large regions showed nonsignificant declines or increases (Table 2). The United States, Canadian, and the North American trends were slightly positive.

Annual indices of abundance.—We present annual indices of abundance for selected states (Fig. 3) and regions (Fig. 4). Annual indices show several patterns of population change among states. Some states are generally increasing (e.g., Georgia and Virginia), while other states are consistently decreasing (e.g., Florida and Vermont). Many states, however, show a quite variable pattern of decline then increase, with the minimum year of either 1978 or an adjacent year (e.g., Alabama, Iowa, Kentucky). FWS Regions 3, 4, and 5 all show generally similar patterns of year-to-year change, with a population minimum in 1978 and high years in 1972 and 1983. United States indices show similar highs and lows and are virtually identical to the North American indices (not shown).

Relative density maps.—The density changes associated with the 1978 population low are strikingly illustrated by the relative density maps (Fig. 5). Density contours shift dramatically between the two maps. Many routes in the central part of the Eastern Bluebird range did not record bluebirds during the population low.

DISCUSSION

Effects of weather.—We have documented a short-term "crash" in Eastern Bluebirds and their subsequent range-wide recovery using BBS data.

←

FIG. 1. Maps of the geographic distribution of increasing and decreasing populations of Eastern Bluebirds for early (1966–78) and late (1978–1987) survey periods from analysis of population trends by physiographic strata.

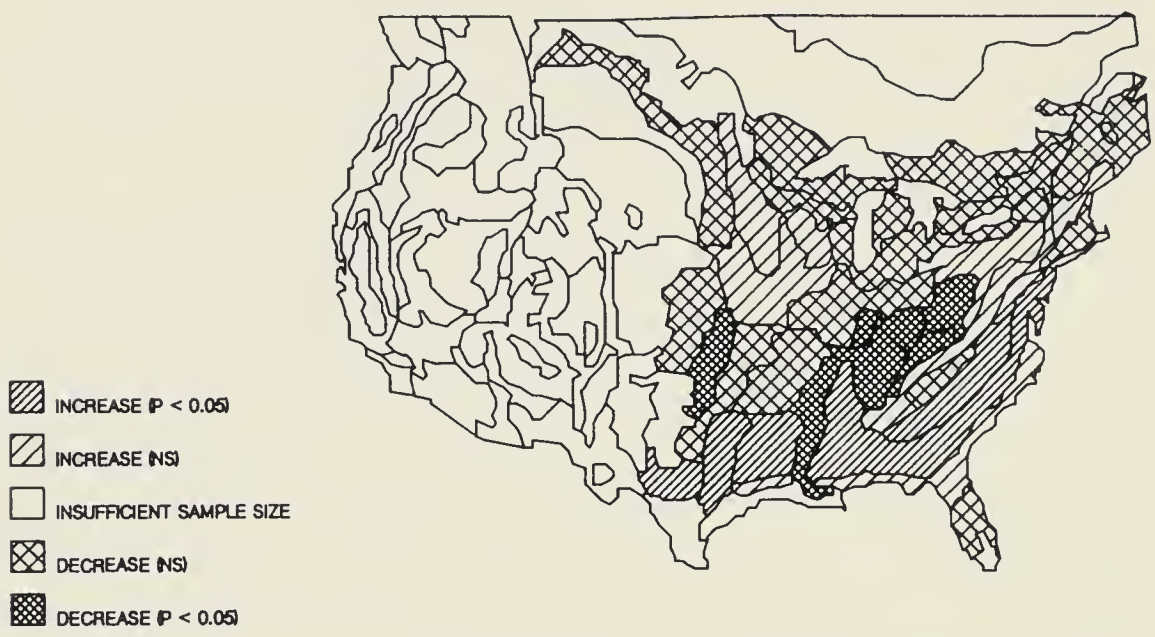
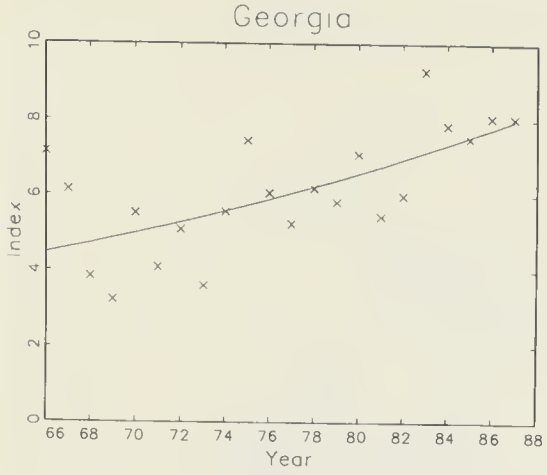
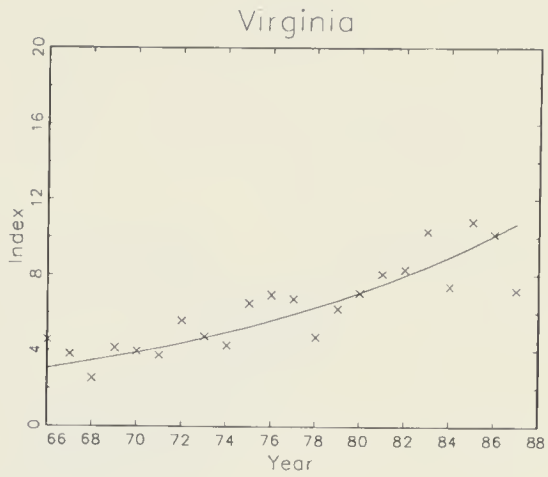


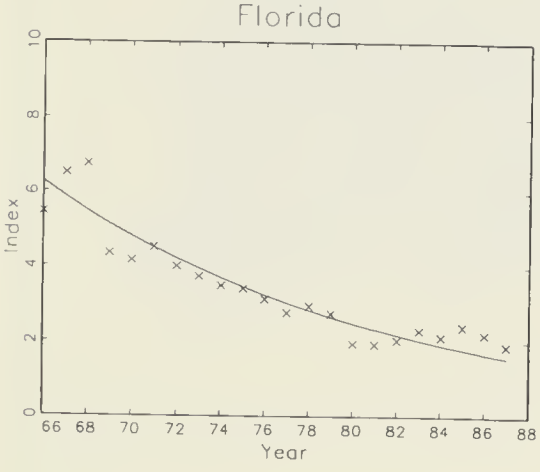
FIG. 2. Map of the geographic distribution of increasing and decreasing populations of Eastern Bluebirds for the 1966–1987 survey period, from analysis of population trends by physiographic strata.

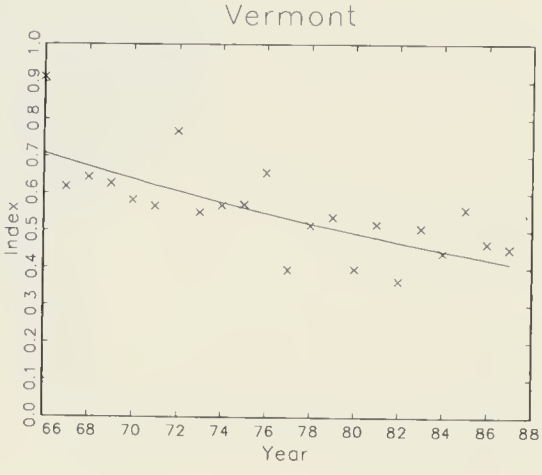
Annual indices of abundance (Figs. 3, 4) provide evidence that extreme declines occurred in many bluebird populations in 1977 and 1978. These large population declines occurred after the 1976–1977 and 1977–1978 winters which were unusually severe (Kerr 1984, Robbins et al. 1986). Rapid declines in Eastern Bluebird populations have been documented for local and regional bluebird populations in the past (e.g., Musselman 1941, Graber and Graber 1979), and these declines are usually associated with severe weather. Robbins et al. (1986) documented an extreme decline in wren populations (especially Carolina Wrens [*Thryothorus ludovicianus*] and Winter Wrens [*Troglodytes troglodytes*]) in the eastern United States in association with severe winters in 1976–77 and 1977–78. These declines were most apparent in the northern portion of the eastern Piedmont, where Eastern Bluebirds also experienced their strongest declines (Fig. 1).

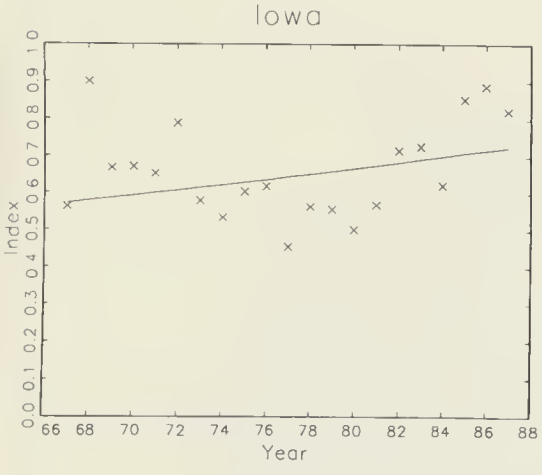
Weather in spring can also influence population changes, as Hurricanes Abbey (in 1968) and Agnes (in 1972) correspond to drops in annual indices of abundance (Figs. 3, 4). These population declines may be due to mortality associated with cold weather during the peak (for Abby) or late (for Agnes) breeding season in spring. Purple Martin (*Progne subis*) populations also experienced population declines in association with these storms (Sauer et al. 1987).

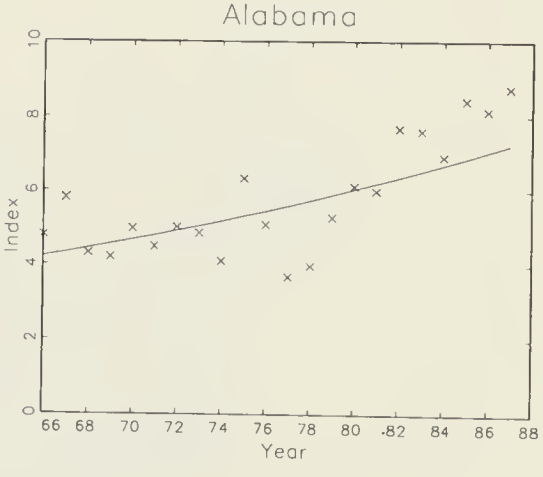












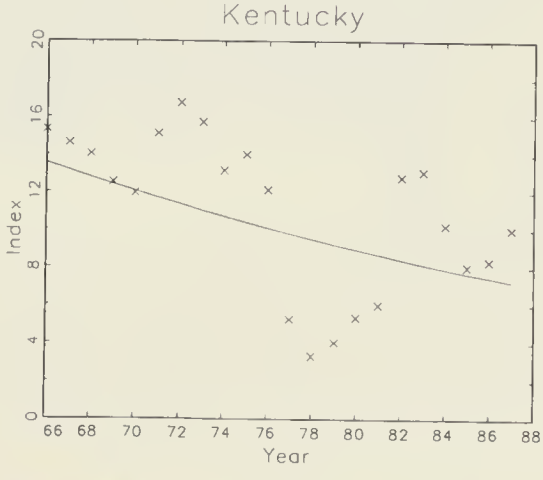


FIG. 3. Annual indices of abundance for selected states from BBS

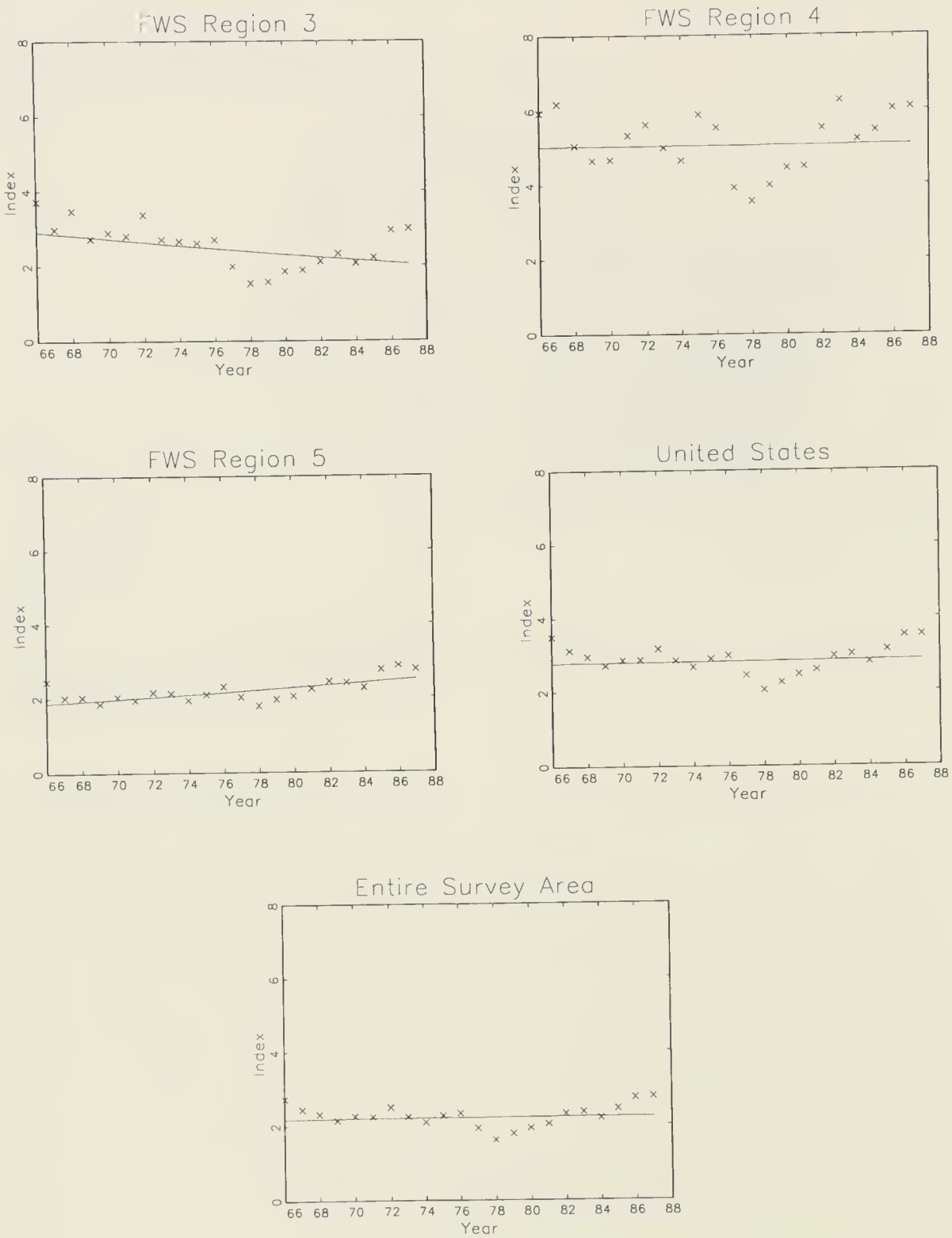


FIG. 4. Annual indices of abundance for selected regions from BBS data.

Population regulation in bluebirds.—Wiens (1977) suggested that bird community structure and species population dynamics are affected by periods of severe climate which keep populations below levels at which competition between species could play a major role in structuring com-

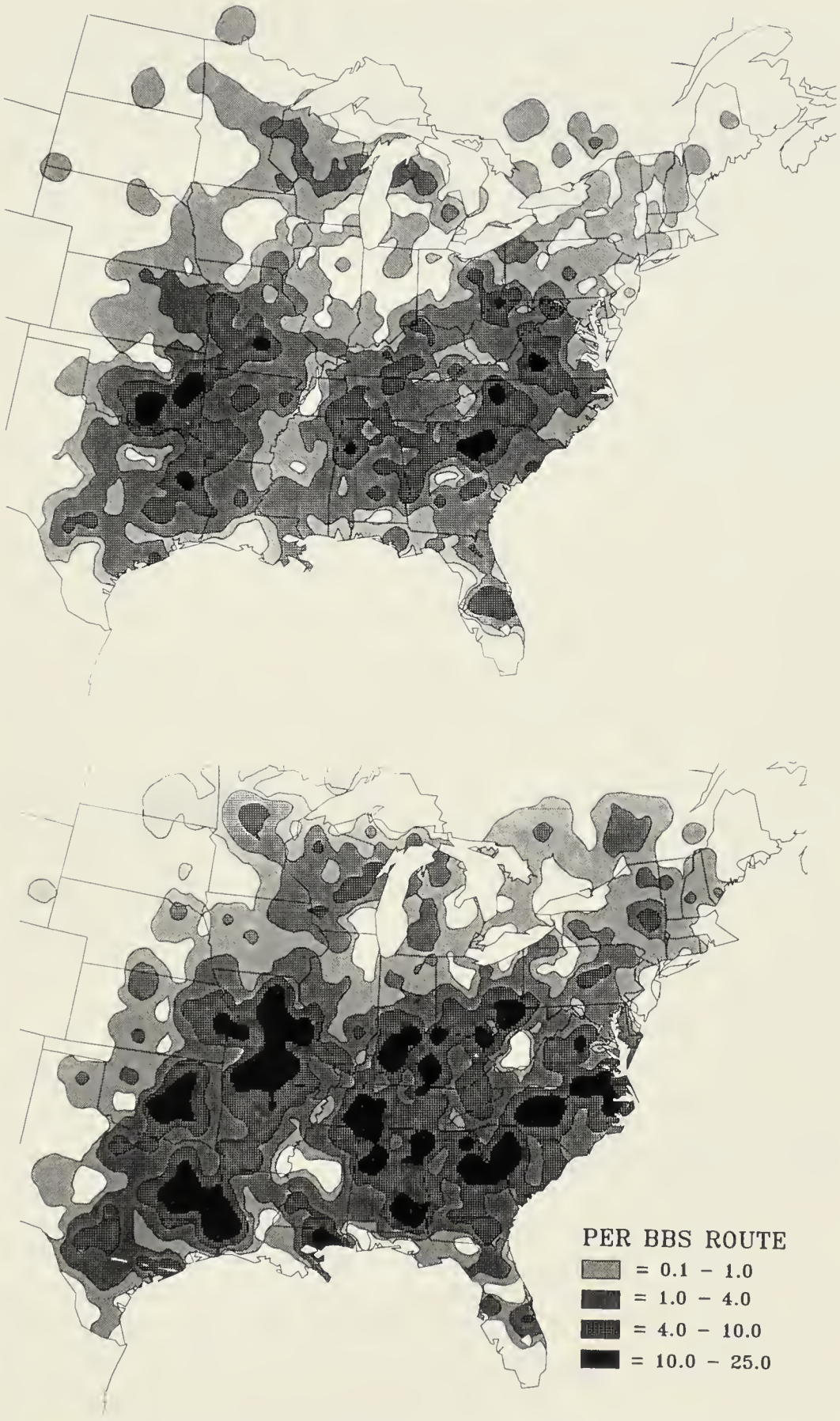


FIG. 5. Relative density contour maps for two time periods: a population low (1977–1979) and a higher density period (1985–1987).

munities. Information from the BBS indicates a short-term decline in the Eastern Bluebird in the 1970s, but a population recovery through the 1980s. These results indicate that Eastern Bluebirds experience "ecological crunches" that, at least in the time period we examined, can dominate bluebird population trends.

Statistical methods exist for the analysis of density-dependency from series of annual censuses (Pollard et al. 1987). It is unclear whether these methods are appropriate for analysis of BBS data because annual indices of abundance may contain both autocorrelation and measurement error which could invalidate the results of the methods (Pollard et al. 1987). However, we note that when this method is applied to annual indices from 35 states and provinces (eliminating states/provinces with extremely low densities) the null hypothesis of complete density independence was rejected in 10 states/provinces. These results suggest that some evidence of density-dependent population regulation exists in bluebirds. However, we feel that analysis of survey data can provide at best limited information regarding the extent and causes of density dependence and that population regulation should be examined through studies of local breeding populations.

Densities of cavity-nesting birds can be limited by the availability of nest sites. Bellrose (1976) determined that Wood Ducks (*Aix sponsa*) were limited by the availability of nesting sites at a study site in Illinois and documented an increase in population size when nesting boxes were placed on the study site. Bluebird populations may have been particularly affected by competition for nest sites (Zeleny 1976), hence the addition of nest boxes throughout the breeding range of the Eastern Bluebird during the 1970s could have influenced bluebird populations. Unfortunately, we do not have information on regional changes in nest-box availability and cannot determine if a correlation exists between changes in nest-box abundance and bluebird population changes.

Short-term versus long-term trends in bluebird populations.—In any fluctuating population, relatively short-term changes tend to mask long-term population trends. For bluebirds, selection of the interval from which trends are estimated can greatly affect the perception of population trend. Earlier analyses of bluebird trends (e.g., Pitts 1981, Robbins et al. 1986) examined an interval corresponding to our early period, when bluebird populations were decreasing. Our analysis of the period 1966–1987 documented no trend, as the population has increased to levels similar to those noted in 1966, when the BBS was initiated. These results emphasize that survey data can be greatly influenced by short-term effects, and population trends estimated from variable populations contain an environ-

mentally induced "noise" component that can sometimes be more evident than a longer-term trend.

Local environmental conditions can cause Eastern Bluebirds to disappear from portions of their range in a relatively short time (Pinkowski 1979, Pitts 1981). However, locally derived data may not reflect regional population changes, and winter severity often varies regionally. Actual regional population changes can be evaluated accurately only by using an extensive survey such as the BBS, which minimizes the bias associated with examination of limited geographic regions.

ACKNOWLEDGMENTS

We thank P. H. Geissler, J. D. Nichols, M. K. Klimkiewicz, and D. Bystrak for reviewing the manuscript. H. Bourne assisted with data manipulation and analysis and prepared several of the figures.

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WINTER HABITAT OF COMMON LOONS ON THE CONTINENTAL SHELF OF THE SOUTHEASTERN UNITED STATES

J. Christopher Haney[1]

Abstract.—Population size, habitat use, and habitat selection of wintering Common Loons (*Gavia immer*) were studied on the southeastern U.S. continental shelf. Winter population estimates ranged from 8700 to 20,000 individuals for the shelf between 29° and 35°N latitude. Loons used shelf waters up to 100 m in depth and 100 km from land. Significant differences in habitat use and selection were found among four shelf habitats differentiated by water depth, distance from land, and water mass properties. Loons selected for waters 0–19 m deep but avoided highly turbid waters within 5–15 km of shore. Loon distribution shifted farther offshore during midwinter, as the areal extent of turbid water increased near shore due to seasonal peaks in river discharge. *Received 21 Oct. 1988; accepted 5 Nov. 1989.*

Considerable concern has been expressed over the population status of the Common Loon (*Gavia immer*). Potential impacts on loons during the nesting season include human disturbance at breeding lakes, acid rain alteration of lake ecosystems, and mercury poisoning of adults (Ream 1976, Titus and Van Druff 1981, Haseltine et al. 1983, Alvo 1986, McIntyre 1986). Die-offs of loons correlated with mercury intoxication have occurred during winter along both the Gulf and Atlantic coasts of the southeastern United States (Alexander 1985).

Very little is presently known about the winter distribution and ecology of Common Loons. Although use of marine waters is well-documented, there are conflicting accounts of whether and to what extent loons use deep, offshore waters on continental shelves (cf. Bent 1919, Cramp and Simmons 1974, Lee 1987). The few dedicated studies of wintering loons have been conducted in sounds and along beach fronts (e.g., McIntyre 1978, Daub 1989). The objectives of this study were to: (1) provide population estimates of wintering Common Loons for the South Atlantic Bight, that area lying between Cape Hatteras, North Carolina, and Cape Canaveral, Florida, and (2) describe marine habitat use and selection by loons within this region. Marine habitat selection was examined as a function of water depth and clarity, environmental variables of potential importance to these visually oriented, diurnal predators (McIntyre and Barr 1983).

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TABLE 1

COMMON LOON USE OF OFFSHORE HABITATS DEFINED BY DEPTH ON THE SOUTHEASTERN U.S. CONTINENTAL SHELF

Habitat	Proportion of survey effort (p_{io})	Number of loon observations	Expected number of loon observations	Proportion observed in each habitat (p_i)	Confidence interval on proportion of occurrence (95% family confidence coefficient)
0–19 m	0.363	55	32	0.625	$0.495 < p_1 < 0.754$
20–39 m	0.269	25	24	0.284	$0.164 < p_2 < 0.404$
40–59 m	0.278	7	24	0.080	$0.008 < p_3 < 0.152$
60–200 m	0.090	1	8	0.011	$0.000 < p_4 < 0.039$
Total	1.000	88	88	1.000	

STUDY AREA AND METHODS

The marine zone between Cape Hatteras, North Carolina, and Cape Canaveral, Florida, is characterized by: (1) the proximity of the Gulf Stream to shelf water masses, (2) a wide (80–160 km) and shallow continental shelf uninterrupted by ledges, banks, or submarine canyons, and (3) the absence of a typical continental slope (Atkinson et al. 1983). Four water masses with different physical and biological properties exist on or near the continental shelf. These water masses are subdivided by depth zones at the 0–20 m (inner shelf), 21–40 m (middle shelf), 41–60 m (outer shelf), and 61–200 m (shelf break) isobaths. Within the inner shelf water mass, a boundary or front (Bowman and Esaas 1978) separates highly turbid water (emanating from coastal estuaries and rivers) from clearer water offshore. The position of the front and the areal extent of turbid water varies with seasonal changes in river discharge rates (Atkinson et al. 1983).

Observations of Common Loons were made during 159 days of seabird surveys in the South Atlantic Bight between May 1982 and June 1985. Survey tracks were mostly opportunistic but frequently repeated among the 43 cruises conducted. All observations were made between 29° and 35°N latitude, primarily on the continental shelf (0–200 m depths). A total of 2476 km^2 was censused using 2118 300-m band transect, 15-min counts (Haney 1986). A fixed-interval rangefinder was used to compute the transect boundary (Heinemann 1981). This method permitted expressing the numbers of loons either as a function of surface area censused or per count hour. Seasonal breakdown of the 15-min counts was as follows: June–August, 664; September–November, 558; December–February, 232; March–May, 664.

Date, latitude and longitude, heading of ship, time of day, visibility, sea height, wind speed and direction, depth, and sea surface temperature were recorded for each count transect. Behavior and, if applicable, feeding associations of loons were also noted during counts and when ships were on station. Loon densities were plotted as a function of depth and distance offshore for all cruises and observations. Seasonal changes in the cross-shelf distribution of loons were plotted in relation to monthly variations in river discharge rates.

Selection and use of marine habitats by loons were examined first by categorizing each loon observation into one of the depth zones described above, using the ship-board LORAN-determined position of the transect. Transects were stratified by habitat categories corresponding to the four principal environmental divisions in the study area (Atkinson et al. 1983) prior to statistical testing. This was done in order to improve inferences about relationships between observational data and environmental measurements (James and Mc-

TABLE 2

COMMON LOON SELECTION OF OFFSHORE HABITATS DEFINED BY DEPTH ON THE SOUTHEASTERN U.S. CONTINENTAL SHELF

Habitat	Proportion of total study area available (p_{io})	Adjusted number of loon observations[a]	Expected number of loon observations	Proportion observed in each habitat (p_i)	Confidence interval on proportion of occurrence (95% family confidence coefficient)
0–19 m	0.336	38	23	0.543	$0.394 < p_1 < 0.692$
20–39 m	0.455	23	32	0.329	$0.189 < p_2 < 0.469$
40–59 m	0.142	6	10	0.086	$0.002 < p_3 < 0.170$
60–200 m	0.067	3	5	0.042	$0.000 < p_4 < 0.102$
Total	1.000	70	70	1.000	

[a] Numbers (Table 1) were adjusted by a scaling factor ($p_{io}/0.25$) to account for differences in census effort among habitat types.

Culloch 1985). Each statistical unit consisted of one or more individual loons observed sitting on the water surface within a transect. Transect length and surface area averaged approximately 4.4 km and 1.4 km^2, respectively. Because these dimensions are considerably larger than individual winter feeding territories of 4–8 ha recorded by McIntyre (1978), transects provided robust and conservative units for subsequent analyses of habitat use and selection.

The proportion of survey effort during fall, winter, and spring months (Nov–Apr) allocated to each habitat (Table 1) was used to test the following hypothesis with the chi-square technique: loon use across all habitats was equal, and thus abundance was in proportion to survey effort. In order to meet the assumptions for calculating a test statistic that was approximately chi-square distributed, the number of habitat categories was chosen so that: (1) there was at least one expected observation in each category, and (2) no more than 20% of all categories contained less than five expected observations (Dixon and Massey 1969: 238). In practice, no categories contained less than eight expected observations for this test.

In a similar fashion, the chi-square test statistic was used to examine habitat selection across all habitat types, i.e., preference or avoidance of habitats with respect to availability. Expected values for this test were determined by calculating the proportion of the total surface area taken by each habitat in the study area (Table 2). Because of differences in survey effort across habitats, the numbers of loon observations were first adjusted by a scaling factor which resulted in fewer total observations (70 vs 88 in the first test; Table 2), but this again provided a robust and conservative test. No categories contained less than five expected observations for the test.

Both chi-square tests considered all habitats simultaneously. To test for use and selection for each individual habitat, the Bonferroni z-statistic was employed (Neu et al. 1974, Byers et al. 1984, Alldredge and Ratti 1986). A set of simultaneous confidence intervals was constructed for the true (observed) proportion of use (p_i) of each of the four habitats in each test. Where the expected proportion of usage (p_{io}) does not lie within this interval, differences between expected and observed use of individual habitats can be identified as significantly different.

Prior to population estimates, distributions of loon counts were tested for normality, skewness, and kurtosis. Populations of Common Loons were estimated by two methods. First, the total numbers of sitting loons were divided by the total surface areas censused for

each habitat. Second, the mean number of loons km^{-2} was computed for each habitat using the total number of transects (including zero count transects) for that habitat. A 90% confidence interval (C.I.) was then figured using standard methods (Bhattacharyya and Johnson 1977). Total numbers of Common Loons for the South Atlantic Bight continental shelf between 29° and 35°N latitude were calculated using mean values and their confidence intervals extrapolated to the total surface area available in each habitat as given in Atkinson et al. (1983).

RESULTS

The chi-square test revealed that use across all four shelf habitats by Common Loons was not equal, i.e., in proportion to sampling allocation ($\chi^2 = 30.98$, $P < 0.005$, df = 3). Loons used the 0–19 m habitat in greater proportion than expected, the 20–34 m habitat within the expected range of probability, and both the 40–59 and 60–200 m habitats in lower proportions than expected by chance (Bonferroni *z*-statistics; Table 1). Similarly, loons selected habitats disproportionately to availability as defined by areal extent ($\chi^2 = 14.71$, $P < 0.005$, df = 3). Loons selected the 0–19 m habitat in greater proportion than expected; however, the three remaining shelf habitats were selected in approximate proportion to their availability (Bonferroni *z*-statistics; Table 2).

Loon abundances also varied across the continental shelf on a finer scale (Fig. 1). Abundances ranged from 1.0 to 3.4 birds km^{-2} within about 5 to 90 km offshore. Very few loons were observed beyond 100 km or in waters deeper than 20 m. A very pronounced decline in offshore abundance occurred near the beginning of the shelf break.

Loons were either rare or absent within a 5–15 km band of turbid water near shore (Fig. 2). The Landsat infrared photograph reveals sediment-laden water emanating from coastal estuaries and Georgia rivers such as the Savannah, Ogeechee, Altamaha, and St. Mary's. Annual discharge of river water varies seasonally, with greater volumes and cross-shelf transport of turbid water during winter and spring. Mean distances from shore and near shore limits occupied by loons retreated farther offshore during these months (Fig. 3).

Count frequencies of loons were not distributed normally in any of the four habitats. Frequency distributions exhibited very high degrees of both kurtosis and positive skewness, a not uncommon trait in at-sea counts of marine birds (Schneider and Duffy 1985). Approximations for computing C.I.'s from non-normal distributions can be made, however, if sample sizes are large (e.g., the inner and middle shelf habitats) (cf. Table 3; Bhattacharyya and Johnson 1977:244).

Population estimates (Table 3) calculated by the total-area-censused method were 13,692 for the inner shelf (0–19 m), 4370 for the middle shelf (20–39 m), 0 for the outer shelf (40–59 m), and 286 for the shelf

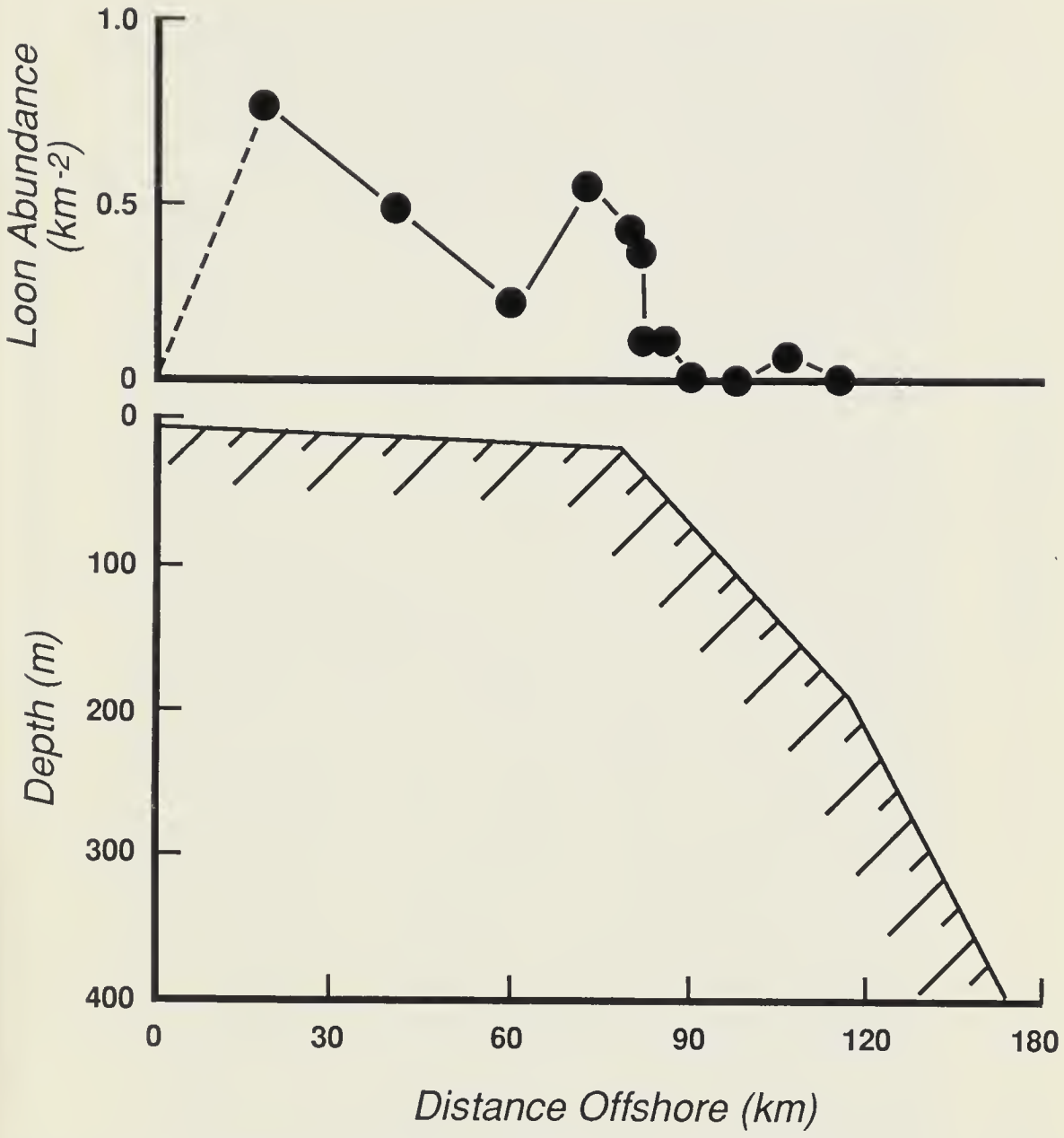

FIG. 1. Cross-shelf abundances of Common Loons off the coast of the southeastern United States. Data points represent mean abundances of loons within twelve ocean depth ranges: 0–5, 6–7, 8–9, 10–11, 12–13, 14–17, 18–20, 21–26, 27–48, 49–69, 70–91, and 92–115 m.

break (60–200 m). Numbers using the mean and 90% C.I. for each habitat were: 10,675 ± 2745 on the inner shelf; 3304 ± 2478 on the middle shelf; 0 for the outer shelf; and 286 ± 429 on the shelf break. Regional estimates for Common Loons on the continental shelf between 29° and 35°N thus ranged from an approximate minimum of 8700 to a maximum of 20,000 individuals.

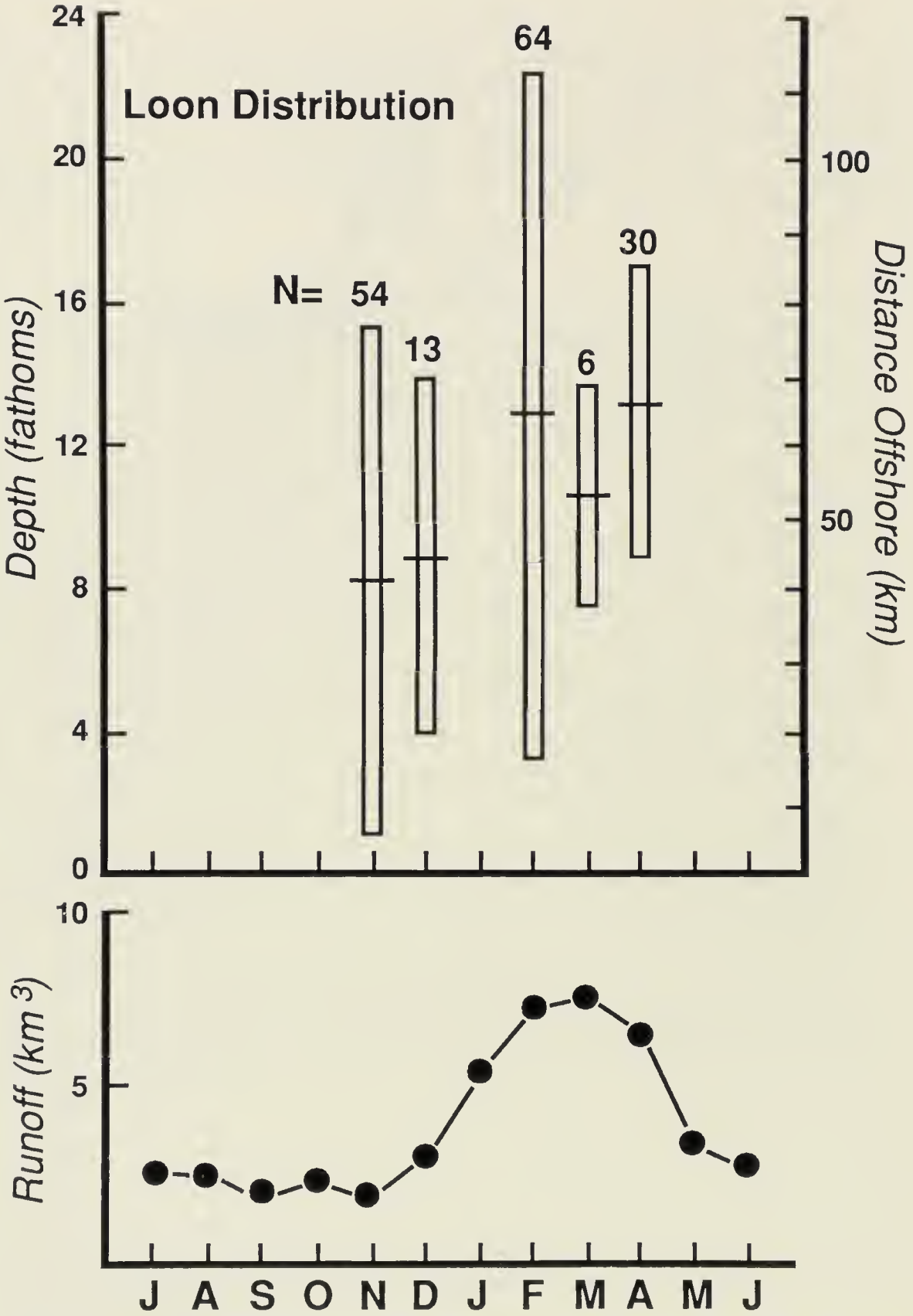

FIG. 2. Seasonal changes in the cross-shelf distribution of Common Loons and their relation to discharge rates of turbid river water. Lines and bars represent mean and SD, respectively; N refers to sample size (number of 15-min, 300 m band transects recording one or more loons).

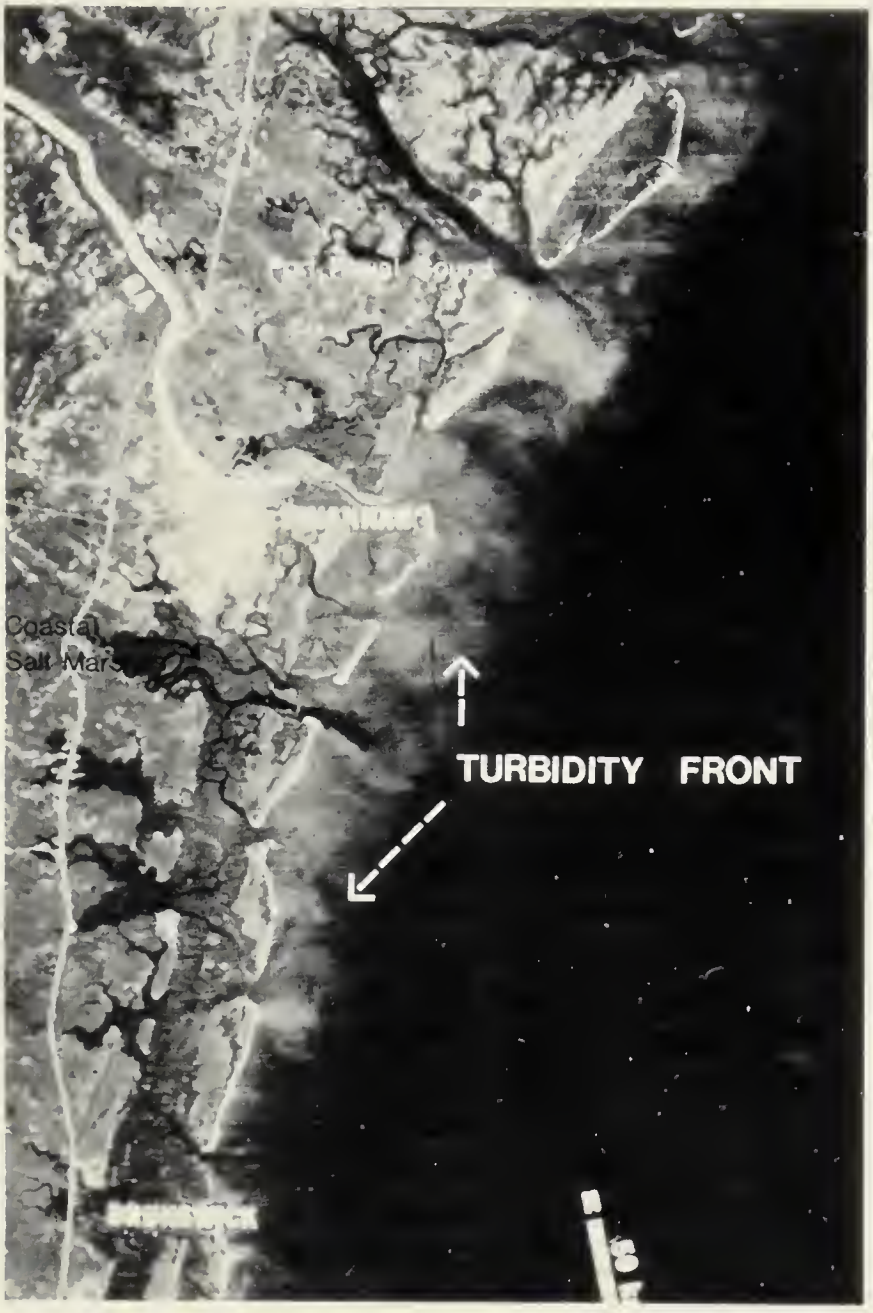

FIG. 3. Infrared image of the Georgia coast taken with thematic mapper aboard Landsat D. The image was taken at 0943 h EST on 9 November 1982 and provided by H. Kim, NASA Goodard Space Flight Center. Note the irregular width and configuration of near shore, turbid waters (light-colored) avoided by wintering Common Loons.

DISCUSSION

Methods used to examine habitat use and selection by wintering Common Loons were in large part dictated by the high variance of the at-sea counts. Because many counts recorded no loons, frequency distributions were highly skewed and non-normal. Because the chi-square technique uses zero counts only for calculating expected probabilities, and because

TABLE 3
POPULATION PARAMETER ESTIMATES OF WINTERING COMMON LOONS LISTED BY HABITAT TYPE

Habitat	0–19 m	20–39 m	40–59 m	60–200 m
Surface area censused (km^2)	347.8	158.8	39.8	41.0
No. loons	145	16	0	1
Density (km^{-2})	0.42	0.10	0.00	0.02
N (no. counts)	310	140	40	37
$\bar{x}$ density (km^{-2})	0.35	0.08	0.00	0.02
SE	0.05	0.04	0.00	0.02
90% C.I.	0.09	0.06	0.00	0.03

it does not require the assumptions of normality as do parametric tests, its use may be advocated in other studies of marine bird distributions (cf. Schneider and Duffy 1985).

Regular occurrence of Common Loons far out at sea was not expected. Cramp and Simmons (1974) state that loons remain within a few kilometers of shore throughout most of their winter range (see also Clapp et al. 1982). However, early accounts (Bent 1919) referred to loons wintering far offshore, and Lee (1987) recently documented loons in winter using waters 20–500 fathoms (ca 40–1000 m) deep and 32–56 km from land off North Carolina. Loons might be expected farther offshore in the South Atlantic Bight because the shelf is broader and more shallow than on the remainder of the eastern North American coastline. Powers and Cherry (1983) found that the offshore distribution of loons was strongly influenced by configuration of the shelf off the northeastern United States, loons being closest to land where the shelf is narrow and farther from land where the shelf is wide.

Relative abundances of wintering Common Loons were higher in the South Atlantic Bight than reported elsewhere in deep marine waters. The number of loons observed varied from 1.00 to 3.44 individuals h^{-1} on the inner and middle shelf compared to 0.34 h^{-1} off North Carolina (Lee 1987) and 0.10 to 1.00 h^{-1} in the northern Chesapeake Bight (Rowlett 1980). McIntyre (1978) reported that wintering loons in a Virginia bay occupied individual feeding territories of 4–8 ha or 12.5–25 birds km^{-2}. This figure is over an order of magnitude higher than densities in the South Atlantic Bight, but shallow and more fertile estuarine habitats may support greater numbers of loons than the deep, relatively impoverished waters of the continental shelf.

Loons on the South Atlantic Bight continental shelf appeared to be limited in both shoreward and seaward directions by the amount of suitable habitat. Loon abundances dropped off sharply where the continental shelf begins to deepen (Fig. 1). This coincides roughly with the maximum diving depths of loons, about 30–40 m (Shoryer 1947). Because loons were observed with benthic fish and crabs in their bills (pers. obs.), deeper water may make some prey inaccessible farther offshore in this region. Lee (1987), however, found a few loons in waters nearly 1000 m deep.

Loons avoided the highly turbid waters near shore (Fig. 3) and moved farther offshore during midwinter (Fig. 2) as turbid water was advected seaward by river discharge. Loons were frequently counted only after ships had crossed turbidity fronts into clearer water. Because loons are diurnal, visually oriented predators, highly turbid water may preclude prey detection. McIntyre and Barr (1983) found a positive correlation between rafting and sunset times, which reinforces the concept that feeding is related to available light levels in the water column. Further studies are needed to determine whether water column turbidity directly influences loon distribution and foraging.

The South Atlantic Bight continental shelf may represent a major wintering ground for Common Loons. On the Atlantic seaboard, few loons winter at sea north of Cape Hatteras (Powers and Cherry 1983). Population estimates of Common Loons from my study ranged from 8700 to 20,000 individuals for the southeastern U.S. continental shelf between 29° and 35°N. Highly turbid water, which loons avoided, is mainly restricted to the central portion of this study area between 30° and 33°N. Because more suitable habitat is present outside the area of high river discharge, these population estimates for the continental shelf tend to be conservative. Numbers of loons may also have been underestimated because of the often obscured viewing conditions at sea or because birds were missed during foraging dives (cf. Tasker et al. 1984).

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EFFECTS OF FOREST IRRIGATION ON LONG-TERM TRENDS IN BREEDING-BIRD COMMUNITIES

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ABSTRACT. — We conducted a long-term study of breeding-bird communities in a deciduous forest irrigated with chlorinated effluent (wastewater) and in a non-irrigated forest in central Pennsylvania. Birds were mist-netted in both forests (sites) each summer during a pre-irrigation era (1978–82) and an irrigation era (1983–87). Community structure and return rates of common species were compared between sites and between eras. Seventy-five species were netted during the ten years. During the pre-irrigation era, no species was significantly more abundant on the irrigated than the non-irrigated site, whereas five species were more abundant on the non-irrigated site. During the irrigation era, five species were more common on the irrigated sites, and four were more common on the non-irrigated site. Four species had lower return rates on the irrigated compared to the non-irrigated site, and two had higher rates on the irrigated site. Based on pairwise comparisons of percent similarity, changes in breeding-bird communities from pre-irrigation to irrigation eras were more dramatic on the irrigated than the non-irrigated site. In particular, bird species diversity and evenness declined on the irrigated site. Most avian responses to wastewater irrigation could be explained by irrigation-induced changes in vegetation. Common Yellowthroats (*Geothlypis trichas*), Indigo Buntings (*Passerina cyanea*), and Song Sparrows (*Melospiza melodia*) were benefited by forest irrigation, but Wood Thrushes (*Hylocichla mustelina*) were negatively affected by irrigation. *Received 13 March 1989, accepted 24 Aug. 1989.*

Human-induced changes in forest habitat can have dramatic effects on food supply, nest sites, singing perches, and cover for birds, consequently altering avian community structure (Johnston 1970, Noon et al. 1979, Maurer et al. 1981, Yahner 1986). The extent of change in avian community structure in an altered environment depends on habitat requirements of individual species in the community (Best et al. 1978).

Irrigation of forests with chlorinated effluent (wastewater) affects plant community structure and composition (Rollfinke 1988), yet little is known regarding the effects of forest irrigation on wildlife. Three previous studies of forest bird communities associated with wastewater irrigation were largely inconclusive because of the small size of experimental plots, short duration of study periods, and irregular or partial-year irrigation schedules (Savidge and Davis 1971, Snider 1974, Lewis and Samson 1981). Thus, relationships between irrigation-induced habitat changes and avian community structure have been inferred but not clearly documented

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(Greenwald 1981). Our objective was to compare long-term trends in breeding-bird communities prior to irrigation with wastewater (1978–82) and during irrigation (1983–87) on an irrigated and a non-irrigated forest in central Pennsylvania.

STUDY AREA AND METHODS

We conducted the study in a forest irrigated with wastewater and in a non-irrigated forest in Centre County, Pennsylvania, from 1978–87 (see details in Rollfinke 1988). The irrigated forest contained a 200-ha wastewater spray-irrigation system, which started year-round operation in April 1983. The system consisted of about 3100 rotating sprinklers connected by a network of pipes that applied about 264 cm of wastewater annually. Average annual precipitation in central Pennsylvania is 93 cm (Matula 1983). The non-irrigated forest was 3 km northwest of the irrigated forest and was part of a contiguous forest tract at the base of Bald Eagle Mountain.

One mist-net site each was established on the irrigated and non-irrigated forests in 1978 (hereafter referred to as irrigated and non-irrigated sites, respectively). Sixteen nets (3.8-cm mesh, 2.1 m × 5.5 m), arranged in a 4 × 4 grid pattern and spaced 30 to 60 m apart, were used at each site to include an area of about 3 ha per site. Both sites included old fields (33%) and deciduous forest (67%) and contained overstory trees from 30 to 60 years old.

Overstory trees (≥7.5 cm dbh) on the irrigated site were primarily quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), scarlet oak (*Quercus coccinea*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), and red maple (*Acer rubrum*). Predominant understory trees (2.5–7.5 cm dbh) and shrubs (<2.5 cm in diameter) included quaking aspen, red maple, rose (*Rosa* spp.), and Tartarian honeysuckle (*Lonicera tatarica*). Major overstory trees on the non-irrigated site included bigtooth aspen, slippery elm (*Ulmus rubra*), hawthorn (*Crataegus* spp.), and white ash (*Fraxinus americana*). Common understory trees and shrubs on the non-irrigated sites were hawthorn, flowering dogwood (*Cornus florida*), common spicebush (*Lindera benzoin*), and Tartarian honeysuckle.

The elevation of the irrigated site was 370–385 m; the non-irrigated site was 365–395 m in elevation. Four ponds formed during the study on the irrigated site; these were about 0.14, 0.13, 0.06, and 0.03 ha in size by summer 1987. There was no standing water on the non-irrigated site, except for a small temporary stream that dried early each summer.

We sampled vegetation at eight random 0.04-ha circular plots per site in summer 1987. Unfortunately, no vegetation data were collected on the two sites prior to irrigation; however, other investigators have documented changes in forest vegetation resulting from operation of this irrigation system (Rollfinke 1988) or its prototypes (Sopper and Kardos 1973, Lewis 1977) within 1 km of our irrigated site. Densities (no./ha) of overstory live trees and snags, stumps (<1.5 m tall, >7.5 cm diameter), logs (≥1 m length, >7.5 cm diameter), and lianas (woody vines ≥1.5 m high, ≥1.0 cm diameter) were determined within each 0.04-ha plot. Densities (no./ha) of understory trees, tall shrubs (≥1.5 m tall), and short shrubs (0.5–1.5 m tall) were quantified in two perpendicular 1-m wide transects within each plot. Percent (%) coverages of herbs, woody vegetation, leaf litter, bare ground, rock, clubmoss, ferns, and logs at ground level and of canopy were determined by taking 20 ocular tube sightings spaced at 2-m intervals along the perpendicular transects. Densities (no./m^2) of tall herbs and ferns (≥0.5 m in height) were determined in four random 1 m^2 subplots within each 0.04-ha plot. Habitat variables were compared between irrigated and non-irrigated sites using Mann-Whitney tests (Sokal and Rohlf 1981). A significance level of $P < 0.05$ was used in all statistical tests.

We mist-netted birds over ten consecutive summers (1978–87) at each site, producing

five years of data both before and during irrigation. Mist-netting was conducted once per week for 13 weeks each summer (early June-late August). The orientation of each mist net was changed from weeks 6 to 9 (generally a 90° pivot around one net pole) to minimize net shyness and to increase capture success (Keyes and Grue 1982).

We opened nets from 0530 to 1100 hours; nets were closed earlier if exposed to direct sunlight on hot days in order to prevent netted birds from overheating (Keyes and Grue 1982). Birds were not netted on mornings with heavy rain or while wastewater was being sprayed (12-h period every 2 weeks). Nets generally were open for 70 h per site each summer. Total net-h were about 1120 per site per year, resulting in over 22,000 net-h during the study.

Each captured bird was identified, aged, sexed (if possible), and banded with a U.S. Fish and Wildlife Service leg band. Birds also were weighed, checked for molt, and measured (mm) for wing, tail, and tarsus length before release. Previously banded birds were classified as "recaptures" if they had been netted earlier that same summer and "returns" if they had been netted in a previous summer. Adult birds (after hatching year), which were netted within the breeding "safe dates" (Gill et al. 1984), were considered resident breeding birds.

Numbers of individuals (C) of each species netted per year (including returning birds banded in earlier years), total number of individual birds of all species combined (N), species richness (S), species diversity (H'), and species evenness (J') were used as measures of community structure and were calculated per year at each site. S = the total number of species; $H' = -\Sigma p_i \log_e p_i$, where p_i is the proportion of individuals of the ith species; and $J' = H'/\log_e S$. C for 18 common species (those with ≥20 resident breeding individuals for all years and both sites combined), N, S, H', and J' were compared between sites and between the two 5-year eras (pre-irrigation and irrigation) using Mann-Whitney tests. Pairwise comparisons of percent similarity (PS) in these resident breeding communities were calculated between eras within a given site and between sites within a given era, where $PS = \Sigma(x_i$ or y_i, whichever is lower), where x_i and y_i are the percent composition of species i in the first and second communities, respectively (Brower and Zar 1984).

Percentages of banded birds that returned in subsequent years were determined at each site for each of the 18 most common breeding species and for all species combined. Return rates were compared between sites using arcsine tests for equality of two percentages (Sokal and Rohlf 1969).

RESULTS

Vegetation differences between sites.—Thirteen and 15 overstory tree species were found on the irrigated and non-irrigated sites, respectively. Overstory trees on the irrigated site had greater dbh ($P < 0.01$) than those on the non-irrigated site (Table 1). Densities of both understory trees and tall shrubs were lower ($P < 0.05$) on the irrigated site than on the non-irrigated site, presumably because of mortality and breakage of trees and shrubs from heavy ice accumulation during winter irrigation (Sopper and Kardos 1973, Rollfinke 1988). Density of herbaceous cover was higher on the irrigated site, but differences between sites were not significant ($P > 0.05$), perhaps because of high within-site variability and small number ($N = 8$) of sampling plots per site (Rollfinke 1988).

Avian differences between sites and eras.—Sixty-nine bird species were netted on the irrigated site and 63 on the non-irrigated site during the ten

TABLE 1

MEANS (± SD) OF SELECTED HABITAT VARIABLES, BASED ON EIGHT 0.04-HA CIRCULAR PLOTS EACH ON AN IRRIGATED AND A NON-IRRIGATED FORESTED SITE, CENTRE COUNTY, PENNSYLVANIA, 1987

Variable	Site	
	Irrigated	Non-irrigated
Overstory tree (all species combined):		
Density (no./ha)	512.5 ± 326.8	409.3 ± 230.0
dbh (cm)	16.4 ± 5.8**	13.6 ± 7.8
Basal area (m^2/ha)	12.1 ± 8.5	7.9 ± 5.9
Understory tree (all species combined):		
Density (no./ha)	603.1 ± 583.3*	1480.3 ± 818.0
Tall shrub (all species combined):		
Density (no./ha)	2467.1 ± 1605.3*	6688.6 ± 3103.1
Short shrub (all species combined):		
Density (no./ha)	13,486.8 ± 7151.3	13,953.9 ± 6223.7
Tall herb/fern (all species combined):		
Density (no./ha)	42,825.0 ± 72,800.0	18,450.0 ± 26,125.0
Physical features: density (no./ha)		
Logs	150.0 ± 157.5	75.0 ± 125.3
Stumps	9.4 ± 12.9	31.3 ± 70.4
Lianas	140.8 ± 151.8	284.5 ± 186.5
Percent (%) coverage:		
Canopy	69.4 ± 28.2	81.3 ± 15.3
Herbaceous ground cover	35.6 ± 19.7	21.3 ± 15.3
Woody ground cover	11.9 ± 16.7	18.1 ± 21.2
Leaf litter	46.9 ± 26.9	39.4 ± 22.6

* $P < 0.05$, ** $P < 0.01$. Significant difference between sites, Mann-Whitney test.

years. Of the 75 species netted on both sites, 56 were species known to breed in the vicinity of our mist-net sites (Wood 1983).

The five most common species on the irrigated site were, in decreasing order of abundance, Song Sparrow (scientific names in Table 2), Gray Catbird, Indigo Bunting, Common Yellowthroat, and Rufous-sided Towhee (Table 2). The most common species on the non-irrigated site were Gray Catbird, Wood Thrush, Red-eyed Vireo, Ovenbird, and Song Sparrow.

During the pre-irrigation era, none of the 18 common species was more abundant on the irrigated as compared to the non-irrigated site, whereas five common species were captured significantly more often on the non-

TABLE 2

TOTAL NUMBER OF INDIVIDUALS NETTED OF 18 COMMON BREEDING SPECIES AND OF ALL SPECIES COMBINED, SPECIES RICHNESS, DIVERSITY, AND EVENNESS OF BIRDS MIST-NETTED (INCLUDING BIRDS BANDED FOR THE FIRST TIME AND RETURNING BIRDS BANDED IN EARLIER YEARS) PER YEAR AT AN IRRIGATED AND A NON-IRRIGATED SITE, CENTRE COUNTY, PENNSYLVANIA, 1978–87

	Era and year											
	Pre-irrigation						Irrigation					
Species	78	79	80	81	82	Mean ± SD	83	84	85	86	87	Mean ± SD
Downy Woodpecker (*Picoides pubescens*)												
Irrigated	6	1	11	9	7	6.8 ± 3.8	4	3	4	10	9	6.0 ± 3.2[b]
Non-irrigated	3	1	1	6	0	2.2 ± 2.4	2	0	1	3	2	1.6 ± 1.1[b]
Black-capped Chickadee (*Parus atricapillus*)												
Irrigated	5	10	6	9	3	6.6 ± 2.9	5	5	7	7	9	6.6 ± 1.7
Non-irrigated	2	7	10	11	9	7.8 ± 3.6	5	6	12	2	6	6.2 ± 3.6
Wood Thrush (*Hylocichla mustelina*)												
Irrigated	12	7	9	6	9	8.6 ± 2.3[a,c]	3	2	2	4	0	2.2 ± 1.5[b,c]
Non-irrigated	19	32	35	18	29	26.6 ± 7.7[a,d]	53	39	38	41	60	46.2 ± 9.8[b,d]
American Robin (*Turdus migratorius*)												
Irrigated	4	1	0	2	4	2.2 ± 1.8	2	5	4	9	4	4.8 ± 2.6[b]
Non-irrigated	0	2	0	1	0	0.6 ± 0.9	0	1	0	0	2	0.6 ± 0.9[b]
Gray Catbird (*Dumetella carolinensis*)												
Irrigated	36	34	40	42	39	38.2 ± 3.2	48	51	38	30	60	45.4 ± 11.7
Non-irrigated	42	52	45	40	35	42.8 ± 6.3	31	43	33	28	31	33.2 ± 5.8
Red-Eyed Vireo (*Vireo olivaceus*)												
Irrigated	0	2	2	3	3	2.0 ± 1.2[a]	4	2	1	1	2	2.0 ± 1.2[b]
Non-irrigated	4	17	5	17	12	11.0 ± 6.3[a]	4	8	10	9	10	8.2 ± 2.5[b]

TABLE 2
CONTINUED

Species	Era and year: Pre-irrigation 78	79	80	81	82	Mean ± SD	Irrigation 83	84	85	86	87	Mean ± SD
Golden-winged Warbler (*Vermivora chrysoptera*)												
Irrigated	1	0	0	3	0	0.8 ± 1.3[a]	0	3	1	0	1	1.0 ± 1.2[b]
Non-irrigated	5	8	4	2	3	4.4 ± 2.3[a]	6	5	2	3	5	4.2 ± 1.6[b]
Worm-eating Warbler (*Helmitheros vermivorus*)												
Irrigated	0	1	3	8	0	2.4 ± 3.4	1	3	1	1	4	2.0 ± 1.4
Non-irrigated	5	3	9	8	0	5.0 ± 3.7	4	6	4	1	5	4.0 ± 1.9
Ovenbird (*Seiurus aurocapillus*)												
Irrigated	6	9	9	4	10	7.6 ± 2.5	9	10	8	6	7	8.0 ± 1.6
Non-irrigated	4	2	6	3	6	4.2 ± 1.8	7	5	15	20	14	12.2 ± 6.1
Common Yellowthroat (*Geothlypis trichas*)												
Irrigated	3	0	6	8	5	4.4 ± 3.1[c]	14	14	12	19	23	16.4 ± 4.5[b,c]
Non-irrigated	4	2	5	1	4	3.2 ± 1.6[d]	8	7	6	10	5	7.2 ± 1.9[b,d]
Yellow-breasted Chat (*Icteria virens*)												
Irrigated	2	4	7	8	0	4.2 ± 3.4	1	6	2	0	0	1.8 ± 2.5
Non-irrigated	5	0	3	0	0	1.6 ± 2.3	0	0	0	0	0	0.0 ± 0.0
Scarlet Tanager (*Piranga olivacea*)												
Irrigated	2	1	0	0	2	1.0 ± 1.0	0	0	1	0	2	0.6 ± 0.9
Non-irrigated	1	6	1	2	8	3.6 ± 3.2	1	3	3	1	4	2.4 ± 1.3
Northern Cardinal (*Cardinalis cardinalis*)												
Irrigated	2	2	8	10	6	5.6 ± 3.6	3	2	4	3	13	5.0 ± 4.5
Non-irrigated	9	4	2	7	10	6.4 ± 3.4	4	6	3	9	13	7.0 ± 4.1

TABLE 2
CONTINUED

Species	Era and year: Pre-irrigation 78	79	80	81	82	Mean ± SD	Irrigation 83	84	85	86	87	Mean ± SD
Indigo Bunting (*Passerina cyanea*)												
Irrigated	3	8	7	11	8	7.4 ± 2.9[c]	16	23	19	29	34	24.2 ± 7.3[b,c]
Non-irrigated	0	0	9	5	9	4.6 ± 4.5	4	3	2	3	4	3.2 ± 0.8[b]
Rufous-sided Towhee (*Pipilo erythrophthalmus*)												
Irrigated	9	9	12	6	10	9.2 ± 2.2	5	7	6	7	11	7.2 ± 2.3
Non-irrigated	7	11	5	5	13	8.2 ± 3.6	6	5	5	10	6	6.4 ± 2.1
Field Sparrow (*Spizella pusilla*)												
Irrigated	7	8	6	6	3	6.0 ± 1.9[a,c]	2	0	0	0	1	0.6 ± 0.9[b,c]
Non-irrigated	10	12	15	7	10	10.8 ± 3.0[a,d]	10	6	5	3	4	5.6 ± 2.7[b,d]
Song Sparrow (*Melospiza melodia*)												
Irrigated	10	5	15	45	27	20.4 ± 16.0[c]	32	52	28	69	116	59.4 ± 35.7[b,c]
Non-irrigated	7	9	11	5	7	7.8 ± 2.3	8	7	5	8	9	7.4 ± 1.5[b]
American Goldfinch (*Carduelis tristis*)												
Irrigated	0	1	2	2	0	1.0 ± 1.0[a]	4	5	3	0	21	6.6 ± 8.3
Non-irrigated	7	1	6	4	7	5.0 ± 2.6[a]	0	4	10	0	1	3.0 ± 4.2
Total number of birds (*N*)												
Irrigated	128	124	187	224	174	167 ± 42	180	221	174	229	384	248 ± 85
Non-irrigated	162	221	212	187	200	196 ± 23	184	200	181	193	201	192 ± 9

TABLE 2
CONTINUED

Species	Era and year: Pre-irrigation 78	79	80	81	82	Mean ± SD	Irrigation 83	84	85	86	87	Mean ± SD
Total number of species (S)												
Irrigated	24	32	30	35	31	30.4 ± 4.0	35	34	33	30	36	33.6 ± 2.3
Non-irrigated	31	41	32	36	34	34.8 ± 4.0	29	33	28	37	28	31.0 ± 4.0
Species diversity (H')												
Irrigated	2.65	2.78	2.96	2.88	2.86	2.83 ± 0.12[c]	2.68	2.60	2.78	2.51	2.60	2.63 ± 0.10[c]
Non-irrigated	2.84	2.94	2.88	3.02	2.96	2.93 ± 0.07	2.66	2.88	2.71	2.90	2.59	2.75 ± 0.14
Species evenness (J')												
Irrigated	0.83	0.80	0.87	0.81	0.83	0.83 ± 0.03[c]	0.75	0.74	0.80	0.74	0.73	0.75 ± 0.03[b,c]
Non-irrigated	0.83	0.79	0.83	0.84	0.84	0.83 ± 0.02	0.79	0.83	0.81	0.80	0.78	0.80 ± 0.02[b]

[a] Significant difference between sites during pre-irrigation era (1978–82), $P < 0.05$, Mann-Whitney test.
[b] Significant difference between sites during irrigation era (1983–87), $P < 0.05$, Mann-Whitney test.
[c] Significant difference between 5-year eras at irrigated site, $P < 0.05$, Mann-Whitney test.
[d] Significant difference between 5-year eras at non-irrigated site, $P < 0.05$, Mann-Whitney test.

irrigated site (Table 2). During the irrigation era, four of the five species (Wood Thrush, Red-eyed Vireo, Golden-winged Warbler, and Field Sparrow) also were more abundant on the non-irrigated site than the irrigated site, but Downy Woodpecker, American Robin, Common Yellowthroat, Indigo Bunting, and Song Sparrow were considerably more abundant on the irrigated site. As a result of three-fold increases in the latter three species, H' and J' declined on the irrigated site during the irrigation era.

Based on *PS*, the breeding-bird community changed more between eras on the irrigated (71% similarity between eras) than on the non-irrigated site (81%). The communities were relatively more similar on the two sites during the pre-irrigation era (66%) than during the irrigation era (53%).

Over 6% of the total birds banded on each site were recaptured in subsequent years (Table 3). Wood Thrush, Red-eyed Vireo, Golden-winged Warbler, and Rufous-sided Towhee had lower return frequencies on the irrigated than the non-irrigated site. Song Sparrow and Gray Catbird had higher return rates on the irrigated site. Northern Cardinal and Field Sparrow had the highest return rates (18% and 17%, respectively, for both mist-net sites combined) of the species studied.

DISCUSSION

Responses of vegetation to installation and implementation of the irrigation system.—Habitat alteration on the irrigated site occurred in two phases. In the first phase, parallel lanes were cleared through the forest for installation of sprinkler lines. These lanes were about 1.2 m (1987) to 4.0 m wide (1978) and were spaced 27 m apart. Thus, tree density was reduced slightly, and narrow gaps in the canopy were created. We feel that habitat alterations resulting from this phase were relatively insignificant compared to that of the second phase.

In the second phase, year-round irrigation of wastewater caused dramatic changes in vegetation. Larger mean dbh of overstory trees on the irrigated than the non-irrigated site was attributed to increased growth rates resulting from added water and nutrients rather than to differences in ages of forest stands between sites (Sopper and Kardos 1973). Ice buildup in winter and a concomitant reduction in densities of understory and shrubby vegetation on the irrigated site presumably decreased the availability of food and cover resources for birds (Lewis and Samson 1981, Rollfinke 1988).

Although density of herbaceous vegetation was not significantly different between sites in our study, others have shown that irrigated forests have taller and lusher herbaceous vegetation than non-irrigated forests (Sopper and Kardos 1973, Mastrota et al. 1990). Further, food resources, such as berries, seeds, and invertebrates, were considerably more abun-

TABLE 3

TOTAL NUMBER OF BIRDS BANDED AND NUMBER AND RATES OF BIRDS RETURNING IN SUBSEQUENT YEARS FOR 18 COMMON BREEDING SPECIES AND FOR ALL SPECIES COMBINED ON AN IRRIGATED (I) AND A NON-IRRIGATED (N) FORESTED SITE, CENTRE COUNTY, PENNSYLVANIA, 1978–87

Species	Site	No. banded	No. returns	Return rate (%)
Downy Woodpecker	I	57	6	10.5
	N	18	1	5.6
Black-capped Chickadee	I	62	3	4.8
	N	62	7	11.3
Wood Thrush[a]	I	54	0	0.0
	N	336	20	6.0
American Robin	I	35	0	0.0
	N	6	0	0.0
Gray Catbird[a]	I	351	41	11.7
	N	346	24	6.9
Red-eyed Vireo[a]	I	20	0	0.0
	N	88	9	10.2
Golden-winged Warbler[a]	I	9	0	0.0
	N	37	5	13.5
Worm-eating Warbler	I	22	0	0.0
	N	45	0	0.0
Ovenbird	I	71	6	8.5
	N	80	2	2.5
Common Yellowthroat	I	92	10	10.9
	N	48	2	4.2
Yellow-breasted Chat	I	30	0	0.0
	N	8	0	0.0
Scarlet Tanager	I	8	0	0.0
	N	30	0	0.0
Northern Cardinal	I	39	9	23.1
	N	56	8	14.3
Indigo Bunting	I	142	10	7.0
	N	37	2	5.4
Rufous-sided Towhee[a]	I	77	2	2.6
	N	57	10	17.5
Field Sparrow	I	29	4	13.8
	N	66	12	18.2
Song Sparrow[a]	I	367	22	6.0
	N	75	1	1.3
American Goldfinch	I	37	1	2.7
	N	40	0	0.0
Total (all species)	I	1852	118	6.4
	N	1797	110	6.1

[a] Significant difference in return rates between sites, $P < 0.05$, arcsine test for equality of two percentages.

dant in irrigated than non-irrigated forests (Lewis 1977, Greenwald 1981, Mastrota et al. 1990).

Avian community response to irrigation.—Avian community structure is associated with vertical and horizontal complexity of forest vegetation (MacArthur and MacArthur 1961, Roth 1976) and local moisture conditions that may affect food supplies (Smith 1977, Swift et al. 1984, Petit et al. 1985). Because the first phase of habitat alteration created by installation of the irrigation system had limited effects on vegetative complexity, we feel that this phase had minimal effects on avian community structure on the irrigated site. Moreover, if clearing of vegetation for pipelines was the primary cause of changes in abundance of the avifauna, these changes would be expected immediately in 1983, which was the year of system installation. Instead, we observed a steady but gradual change in avifauna subsequent to system installation, corresponding with changes in vegetation structure. Thus, we contend that changes in avifauna between the two sites were attributed principally to the second phase of habitat alteration, i.e., irrigation, which increased habitat heterogeneity and reduced habitat for forest specialists.

In general, we found avian responses to forest irrigation with wastewater to be more dramatic than suggested in earlier studies. Savidge and Davis (1971) found no significant changes in an avian community associated with a young woodlot with over five years of irrigation, except for an increase in American Robins. Both Snider (1974) and Lewis and Samson (1981) reported significantly lower breeding-bird densities on irrigated mature oak sites than on undisturbed mature sites; however, they found increased avian densities in irrigated young aspen-pine (*Pinus*) stands. We found a dramatic increase in total bird numbers on the irrigated site after the onset of irrigation, primarily because several forest-edge species became much more abundant relative to other species. In addition, species composition on the irrigated site during the irrigation era was very dissimilar (*PS*) compared to that on the irrigated site prior to irrigation or to community structure on the non-irrigated site in either era.

Avian species richness (*S*) often declines in stressed or disturbed ecosystems (Adams and Barrett 1976). Evenness (*J'*), on the other hand, is relatively stable and usually does not fluctuate markedly in response to habitat changes (Kricher 1972, Adams and Barrett 1976). Especially in summer, species diversity (*H'*) varies primarily as a function of species richness and is influenced minimally by species evenness (Rotenberry et al. 1979). In our study, however, species diversity declined with the onset of irrigation on the irrigated site not because of a decrease in richness but because the avian community became dominated by a few forest edge species, causing a significant decline in *J'*.

Individual species responses to irrigation.—Wastewater irrigation of the forest increased the abundance of edge species, particularly Common Yellowthroats, Indigo Buntings, and Song Sparrows. Yellowthroats and buntings have shown recent population increases in much of the eastern U.S. (Anderson et al. 1981, Robbins et al. 1986), where extensive habitat fragmentation has created increasing amounts of edge (Yahner 1988).

Yellowthroats nest and forage in areas of dense low vegetation, which is typical of moist habitats (Stewart 1953, Yahner 1987). Sedgwick and Knopf (1987) suggested that yellowthroat populations can serve as ecological indicators of the quality of ground/shrub vegetation. Indigo Buntings and Song Sparrows similarly are ground/shrub-foragers associated with dense brushy vegetation and usually are absent from closed-canopy forests (DeGraaf et al. 1980, Maurer et al. 1981, Kahl et al. 1985). Lush growth of herbaceous vegetation and formation of ponds associated with the installation and operation of the irrigation system provided suitable habitat for these species on the irrigated site.

We found that wastewater irrigation may be detrimental to populations of Wood Thrush. Lewis and Samson (1981), however, noted that thrushes increased in a young irrigated forest but decreased on an irrigated mature site. Wood Thrushes prefer forests with moderately dense understory/subcanopy layers because they nest in saplings and shrubs (DeGraaf et al. 1980, Kahl et al. 1985). Thus, winter ice damage to understory trees and shrubs may reduce the availability of nesting sites for thrushes in irrigated forests. Further, because Wood Thrushes methodically forage at ground level (Holmes and Robinson 1988), dense herbaceous growth in irrigated forests may reduce foraging efficiency of this species.

Return rates.—Return rates reflect survival and site fidelity of breeding birds. Van Horne (1983) has recommended that habitat quality for a species be defined in terms of survival as well as abundance. Lower rates of return of banded birds on the irrigated site compared with the non-irrigated site suggest that habitat quality for Wood Thrushes, Red-eyed Vireos, Golden-winged Warblers, and Rufous-sided Towhees was lower on the irrigated site. Red-eyed Vireos and Golden-winged Warblers were not abundant on the site even before irrigation began; thus, the site initially may have been marginal for those species. Lower return rates for Wood Thrushes in the irrigated forest lend support to our previous conclusion that habitat quality declined for this species with the installation and operation of the wastewater system. The lush herbaceous growth in the irrigated forest also may have impacted Rufous-sided Towhees which nest and forage on or near the ground (e.g., Yahner 1987), although their abundance did not change. Higher return rates on the irrigated site for Gray Catbirds and Song Sparrows likely indicate that habitat changes

benefited these species, but only Song Sparrows increased significantly in abundance.

Although overall return rates (6.3% for both sites combined) did not differ between irrigated and non-irrigated mist-net sites, these values compared favorably with other studies. Blake (1953) reported a 6.7% return rate for breeding songbirds in Massachusetts. Baumgartner (1986) reported a slightly higher return rate of 8.7%, but her totals included wintering birds attracted to feeders and caught in traps rather than mist-nets. In a two-year study of wastewater-irrigated habitats, Snider (1974) had a 4.9% return rate between years.

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INTRASPECIFIC BROOD PARASITISM IN THE EUROPEAN STARLING

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ABSTRACT.—We studied intraspecific brood parasitism in the European Starling (*Sturnus vulgaris*) in New Jersey. We used three criteria to detect brood parasitism. These were: (1) the appearance of more than one egg/day while the host was laying, (2) the appearance of extra eggs after the host completed its clutch, and (3) the mismatching of protein phenotypes between parent and putative offspring using polyacrylamide gel electrophoresis of blood and pectoral muscle tissue. Based on these methods of detection, one in every four early nests (i.e., clutches initiated in April) contained at least one parasitic egg. Later nests experienced little parasitism. Hosts from parasitized nests of the electrophoresis sample fledged fewer young than nonparasitized nests. Hosts exhibited behaviors that minimized the potential cost of brood parasitism. These behaviors included throwing out the first parasitic egg, initiating incubation midway through laying, laying synchronously, and laying one less egg than the apparent optimal clutch size. Parasites searched for unattended nests in which to lay their eggs. Those parasites laying eggs synchronously with the population fledged more young than those that did not. However, parasites probably laid only one egg to the hosts' four or five. Parasites were probably birds without nests and were therefore adopting a reproductive strategy that was better than total reproductive failure. Intraspecific brood parasitism may be an evolutionary force shaping the current reproductive strategies of our population of European Starlings. *Received 22 Dec. 1988, accepted 27 Aug. 1989.*

Intraspecific brood parasitism (i.e., laying in the nest of an unrelated conspecific host with no subsequent care of egg[s] or offspring) in altricial birds has often been reported anecdotally in the literature (e.g., Kessel 1957, Victoria 1972, Weatherhead and Robertson 1978, Dhindsa 1983). With the advent of electrophoresis, cases of parasitism that would otherwise have remained undetected have been revealed (e.g., Evans 1988, Gowaty and Karlin 1984, Fleischer et al. 1985, Kendra et al. 1988) and suggest that intraspecific brood parasitism in altricial birds is more common than previously thought.

Beyond assessing the frequency of intraspecific brood parasitism, some studies have shown that this behavior may have adaptive value for the parasite. Brown and Brown (1989) have shown that parasitic Cliff Swallows (*Hirundo pyrrhonata*) may produce more young than hosts. Emlen and Wrege (1986) have shown that White-fronted Bee-eaters (*Merops bullockoides*), whose breeding has been interrupted, will parasitize other nests. By doing so, they may regain the chance of fledging young.

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Intraspecific brood parasitism exploits a valuable resource, parental care, and therefore can affect the evolution of parental care and associated behaviors (Hamilton and Orians 1965, Payne 1977). The role of natural selection in shaping the interactions between hosts and parasites was addressed by Brown and Brown (1989). Rather than viewing intraspecific brood parasitism as a random act with little consequence, Brown and Brown (1989) suggest that the behaviors of hosts and parasites have shaped the present reproductive strategies of the population.

We examined intraspecific brood parasitism in an altricial species, the European Starling (*Sturnus vulgaris*), breeding in New Jersey. Other reports of intraspecific brood parasitism in the starling have been both anecdotal (Kessel 1957, Yom-Tov et al. 1974, Power et al. 1981) and well-documented (Evans 1988). Discrepancies in egg-laying patterns and electrophoretic analysis of families enabled us to determine that intraspecific brood parasitism is widespread in our population and not favorable to the reproductive success of hosts. Several behaviors of hosts and parasites suggested that the interactions between hosts and parasites influence the reproductive strategies found in our population of starlings.

METHODS AND MATERIALS

This study was conducted from 1983–1985 on the Kilmer Campus of Rutgers University in Piscataway, New Jersey, on a population of starlings under observation since 1975 (Crossner 1976, Power et al. 1981). Wooden nest boxes were placed on utility poles located along roadways. Utility poles were three to four territory diameters apart (one territory diameter = 10 m; Feare 1984). Vegetation in and around the field site consisted of mowed lawns and scrub and brush. To protect against mammalian predators such as raccoons (*Procyon lotor*) and gray squirrels (*Sciurus carolinensis*), aluminum predator guards 0.61 m wide were placed around all poles directly under the box. In 1983 there were 30 boxes, in 1984 50 boxes, and in 1985 75 boxes.

Three of Yom-Tov's (1980) criteria were used to detect parasitic eggs: (1) The appearance of more than one egg/day before the host completed its clutch indicated that at least two females were laying. Birds normally lay no more than one egg in a day (Warren and Scott 1935, Woodard and Mather 1964, Fraps 1965). (2) The appearance of eggs after the host completed its clutch indicated that another female had laid an egg in a nest after the host was physiologically incapable of further laying (Bullough 1942). Bullough showed that the ovaries of starlings regress rapidly after the completion of a clutch. This was confirmed for our population when post-laying ovaries removed from 52 starlings two to three days after apparent clutch completion showed no active follicles (Kennedy et al. 1989). (3) Genetic nonrelatedness was indicated when there was a mismatch of proteins between putative parents and offspring as detected by electrophoretic analysis.

Nests were checked during the breeding season (mid-April through mid-July). Censuses were performed once daily beginning on 15 April until the first eggs appeared (19 April for all years). Thereafter, nests were checked twice daily in 1983 and 1984 (in the morning and early afternoon) and three times daily in 1985 (07:00–08:00 EST, 11:00–12:00 EST, and 16:00–18:00 EST). In all years, each April clutch was checked at least twice daily until two days after the host completed its clutch. Clutches were considered complete when no new

eggs appeared in the nest for two consecutive days. Thereafter, clutches were checked irregularly until hatching, which occurred approximately 12 days after the onset of incubation. The onset of incubation was determined by touching the eggs with the back of the hand to detect warmth (Power et al. 1981). Clutches started after April were checked once daily until completion and irregularly until hatching.

Eggs were numbered sequentially with indelible ink when first detected. In order to maintain the identity of nestlings from egg to fledging, unhatched nestlings were dyed with commercially available food coloring at the time of pipping (Rotterman and Monnett 1984). (This was done in 1984 and 1985 only.) The toenails of newly hatched nestlings were clipped in a unique pattern that allowed identification of their position in the egg-laying sequence for the duration of the nestling period (Romagnano 1987). Broods were visited irregularly until Day 18, at which time nestlings were prevented from fledging until Day 20 (nestlings fledge on or about Day 20; Day 1 = day of hatching of the first egg). To restrict nestlings from fledging but still allow parents to feed, a small rectangular piece of wood with a circular opening of 2.54 cm was placed over the nest box entrance; the entrance itself had a diameter of 5.08 cm. This was done to facilitate tissue collection for electrophoretic studies (see below). After Day 20, the wooden "restrictors" were removed. Nests were visited daily until the fate of all was ascertained (Hoffenberg et al. 1988).

Both blood and pectoral muscle tissue were collected from families for polyacrylamide gel electrophoresis of native proteins. Adult females were captured, banded, and biopsied while brooding young on the sixth night after the first nestling hatched. Only resident females brood young during the night, thus assuring capture of the "correct" female (Litovich 1982). Adult males were captured, banded, and biopsied the next day while feeding young. A radio controlled trap modified from the design of Lombardo and Kemly (1983) was used to capture males in the nest. Nestlings were biopsied on Day 20. See Hoffenberg et al. (1988) for details of tissue collection and preparation and electrophoresis protocols.

Thirty-three presumptive loci were screened in plasma, hemolysate, and pectoral muscle. Three loci were found to be genetically variable and resolvable (Romagnano et al. 1989). These were plasma amylase (two alleles), pectoral muscle esterase 1 (three alleles), and pectoral muscle esterase 2 (two alleles) (Romagnano 1987, Hoffenberg et al. 1988).

A genetic mismatch was considered a case of unambiguous intraspecific brood parasitism if a nestling phenotype mismatched both putative parents or the putative mother only, e.g., if the nestling displayed a BB phenotype and both parents (or the putative mother only) were AA. A genetic mismatch was considered a case of cuckoldry (Power et al. 1981) if the nestling mismatched only the putative father and there was no field evidence of parasitism (see below). Other classes of mismatches were considered ambiguous. One such class consisted of a nestling that partly mismatched both of its putative parents (e.g., a nestling with an AB phenotype and AA parents could have been the result of either cuckoldry or parasitism). Another ambiguous class consisted of a mismatch between a nestling and its putative father in which there was field evidence of the possibility of parasitism. Field evidence included variation in egg shape or color within the clutch (Feare 1984, Evans 1988), egg removal at the nest (parasites sometimes remove eggs preparatory to or while laying their own eggs (Evans 1988, Lombardo et al. 1989), and occurrence of unambiguous cases of parasitism at the same nest, showing that the parasite was active there. Despite such evidence, some cases could not be determined to be either parasitism or cuckoldry, and hence were left in a category called "unassigned" (Hoffenberg et al. 1988).

Clutches were partitioned into three types based on population peaks of laying. These were early clutches (initiated in April), intermediate clutches (initiated in May), and late clutches (initiated in June).

Data were partitioned into two population samples based on methods of data collection.

TABLE 1

FREQUENCY OF BROOD PARASITISM BY YEAR AND CLUTCH TYPE FOR THE CENSUS SAMPLE

	Early				Intermediate				Late			
	N[a]	PL[b]	PA[c]	%[d]	N	PL	PA	%	N	PL	PA	%
1983	22	2	1	13.6	13	0	0	0	2	0	0	0
1984	44	5	5	22.7	21	0	0	0	23	1	1	8.7
1985	45	13	5	35.6[e]	41	1	3	9.8	30	1	0	3.3
Total	111	20	11	26.1[e]	75	1	3	5.3	55	2	1	5.5
				(40)[f]				(5)				(3)

[a] Total number of clutches.
[b] Number of clutches parasitized while the host was laying.
[c] Number of clutches parasitized after the host completed its clutch.
[d] Percent of clutches parasitized.
[e] Two nests contained parasitic eggs laid both during and after host laying.
[f] Numbers in parentheses indicate the number of parasitic eggs.

The census sample included all clutches that were checked on a daily basis for parasitic eggs. These clutches did not necessarily survive to fledging. The electrophoresis sample (a subset of the census sample consisting of only those clutches whose nestlings survived to be biopsied) included those clutches that were both checked on a daily basis for parasitic eggs and sampled for electrophoretic analysis.

Parasitic eggs were partitioned into two types: those laid while the host was laying and, therefore, likely to hatch and fledge, and those laid after the host completed its clutch and, therefore, not likely to hatch or fledge.

The term "reproductive success" refers to the number of fledglings resulting from a breeding attempt by either hosts or parasites. The term "cost" refers to the loss of fledglings.

RESULTS

Frequency and patterns of occurrence: census sample.—For all three years, 241 clutches were checked for parasitic eggs. On the basis of more than one egg/day and the appearance of eggs after the host completed its clutch, parasitism occurred at 36 nests (48 eggs) with an increase in rate from year to year (Table 1). Early clutches experienced the greatest rate of parasitism (26.1%) with dramatic declines in rates for intermediate and late clutches. More nests were parasitized while the host was laying than after.

There was no evidence that nest checking increased the rate of parasitism by disturbing laying birds and causing them to desert (deserting birds may attempt to lay their eggs in the nests of other birds). Only two cases of nest desertion were attributed to nest checking. In addition, only five nests experienced gaps in their laying sequence, suggesting that nest checking did not cause wholesale temporary desertions. Moreover, these gaps may have been due to egg removal by parasites (Lombardo et al. 1989).

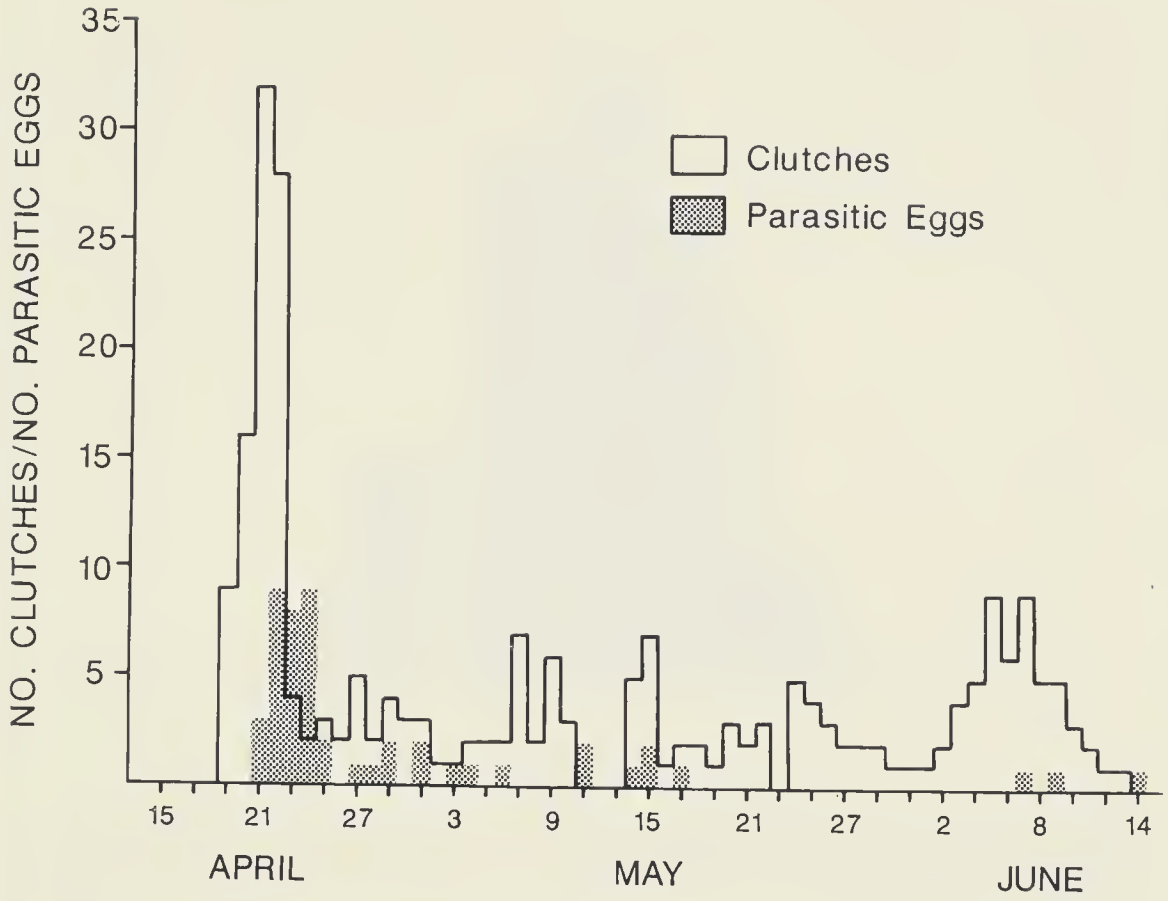

FIG. 1. Dates of clutch initiation (N = 238) and appearance of parasitic eggs (N = 49 including 5 eggs detected by electrophoresis).

Most parasitic eggs coincided with the first peak of laying (Fig. 1). These clutches fledged more young than intermediate or late clutches (Table 2). In addition, most parasitic eggs laid before the host completed its clutch were laid on Days 2 and 3 of the host's laying cycle (Fig. 2). The modal starling clutch was five eggs. Incubation usually started on the third day of laying (Fig. 3). Hatching consequently occurred over a period of two or three days, when clutches were larger than three.

Seventy-six percent of all early eggs (N = 239) from nonparasitized clutches from 1985, the year the time of laying could best be detected, were laid between 07:00 and 11:00 (i.e., detected at the 11:00 census), 6.3% were laid between 11:01 and 16:00 (i.e., detected at the 16:00 census), and 17.6% were laid between 16:01 and 06:59 the next day (i.e., detected at the 07:00 census). However, of 18 parasitic eggs laid while the host was also laying 10 (56%) were detected at different censuses than the ones during which the host's eggs were detected.

Frequency and patterns of occurrence: electrophoresis sample.—A total of 185 adults (102 females and 83 males) and 365 nestlings were biopsied for all years and clutch types. A total of 118 families were analyzed

FIG. 2. Day of appearance of parasitic eggs (N = 31 including 5 eggs detected by electrophoresis) with respect to the host's laying cycle. The eggs were not evenly distributed over a five day laying cycle ($\chi^2 = 30.78$, df = 4, $P < 0.001$).

electrophoretically. (Of these, 106 were complete for male, female, and nestlings.) The number of families exceeded the number of males and females biopsied because some birds had more than one brood either within a year or between years.

The frequencies of the alleles at the three loci used for parental exclusion were 0.52 and 0.48 for plasma amylase; 0.92, 0.04, and 0.04 for pectoral muscle esterase 1; and 0.96 and 0.04 for pectoral muscle esterase 2. All loci were determined to be in Hardy-Weinberg equilibrium and to assort independently (Romagnano 1987, Hoffenberg et al. 1988).

Six cases of parasitism were detected electrophoretically in five of 72 early broods (6.9%), all on the basis of amylase (Hoffenberg et al. 1988). Two of the parasitism cases were detected at one nest. One of these was detected by both nest checking and electrophoresis. (The relative efficiency of electrophoresis vs nest checking is discussed in Romagnano et al. (1989)). Six additional mismatches were also detected but could not be unambiguously assigned as cases of parasitism. Two nests contained nestlings resulting from cuckoldry (Hoffenberg et al. 1988).

Fifteen additional early broods in the electrophoresis sample were also parasitized but detected by nest checking only (Table 3). The total rate

FIG. 3. Day in laying cycle (N = 219 nests) when incubation was begun. Nests with warm eggs two days in a row were considered to have begun incubation on the first of the two days.

of brood parasitism was 27.8% for early broods (20 of 72 early broods). As with the census sample, more nests were parasitized while the host was laying than after.

Effect of brood parasitism on hosts.—Post-laying parasitism often occurred during incubation or after hatching. Since these eggs never fledged they had little or no effect on the reproductive success of the host. Thus, only parasitism during laying was important to the host. Only clutches where the fate of all eggs was known, and clutches that did not experience

TABLE 2

MEAN CLUTCH SIZE, HATCHLING AND FLEDGLING NUMBER FOR ALL CLUTCH TYPES OF THE CENSUS SAMPLE, INCLUDING PARASITIC EGGS

	Clutch size		Hatchlings		Fledglings	
	Mean	SD	Mean	SD	Mean	SD
Early	4.99	0.852	3.77	1.47	2.54	1.71
Intermediate	4.43	1.09	3.43	1.53	1.43	1.54
Late	3.80	0.826	2.69	1.36	0.96	1.30

TABLE 3

FREQUENCY OF BROOD PARASITISM BY YEAR AND CLUTCH TYPE FOR THE ELECTROPHORESIS SAMPLE

	Early				Intermediate				Late			
	N[a]	PL	PA	%	N	PL	PA	%	N	PL	PA	%
1983	12	1	0	8.3	0	—	—	—	0	—	—	—
1984	30	3	5	26.7	9	0	0	0	6	0	1	16.7
1985	30	11[b]	2	36.6[c]	18	0	3	16.7	13	0	0	0
Total	72	15	7	27.8[c]	27	0	3	11.1	19	0	1	5.3
				(28)				(4)				(1)

[a] Symbols as in Table 1.
[b] Five nests contained parasitic eggs detected by electrophoresis.
[c] Two nests contained parasitic eggs laid both during and after host laying.

loss of eggs or hatchlings due to human interference, are included in the following three analyses. No significant differences were found between the mean number of host's young fledged from early clutches that were parasitized (N = 14) and clutches that were not parasitized (N = 66) in the census sample (Mann-Whitney *U*-test; $U = 346.5$, $P > 0.10$). In contrast, the electrophoresis sample showed significantly fewer host's young fledged from parasitized (N = 13) tha nonparasitized (N = 47) early clutches (Mann-Whitney *U*-test: $U = 136$, $P < 0.01$).

Clutches of four or smaller are often laid by yearlings (Flux and Flux 1981, Feare 1984). These inexperienced breeders might be more affected by brood parasitism if they are not able to care for a larger clutch. However, the mean number of fledglings from host's eggs was the same for parasitized clutches ≤ 4 and ≥ 5 (Mann-Whitney *U*-test; $U = 9.5$, $P > 0.10$ and $U = 9.5$, $P > 0.10$ for census and electrophoresis samples, respectively).

Relative efficiency of brood parasitism as a reproductive strategy.—Of the 26 parasitic eggs laid in early clutches while the host was also laying, 13 (50%) fledged in the census sample. This is the same fledging rate as for early eggs from nests that were not parasitized (N = 544 of which 41% fledged) ($\chi^2 = 0.795$, df = 1, $P > 0.30$). However, there was a significant difference between the fledging rate of parasitic eggs laid while the host was laying and those laid after (0%) ($\chi^2 = 9.66$, df = 1, $P < 0.01$).

Of the 53 parasitic eggs detected by censusing and/or electrophoresis, 45 occurred singly in nests (84.9%). Multiple parasitism (i.e., the dumping of more than one egg per host nest) occurred at only five of 111 early nests (4.5%). There was no evidence that any one parasitic female was able to lay a complete clutch (4–6 eggs) in any one nest or in several nests.

However, at two nests egg weight and appearance strongly suggested only one parasite for each of the three parasitic eggs at those nests.

During early laying, many eggs were found on the ground either directly below or between nest boxes (Lombardo et al. 1989). Stouffer et al. (1987) found that parasitic eggs laid before the host initiated its clutch were always removed by hosts. This decreased the reproductive success of brood parasites relative to nesting starlings. The actual number of parasitic eggs is probably under-represented because eggs found on the ground were not counted as such.

DISCUSSION

The high frequency of intraspecific brood parasitism in our population has led to some apparent behavioral adaptations on the part of both hosts and parasites. This suggests that intraspecific brood parasitism is a driving evolutionary force that has allowed the coexistence of two alternative, but opposing, reproductive strategies.

The cost of brood parasitism could act as a selective pressure encouraging changes in reproductive behavior. The cost to hosts in the electrophoresis sample was not apparent in the census sample. This could be a function of the methods of data collection. The census sample included both broods that survived to fledging and broods that failed, often for reasons other than parasitism (e.g., weather). The electrophoresis sample included only those families that survived to biopsy. Relative to the census sample, the families of the electrophoresis sample were more likely to experience the detrimental effects of competition between host's young and parasitic young. The electrophoresis sample was thus more likely to demonstrate the effects of parasitism on the reproductive success of hosts.

Reduced fledging success could occur if the host was forced to raise a brood that had been increased beyond optimal size due to the addition of one or more parasitic eggs. Oversize clutches might be more difficult to incubate (Biebach 1981, Westerterp et al. 1982) or to feed (Crossner 1977, Tinbergen 1981). Also, the survival chances of specific host nestlings (e.g., last hatched young) might be decreased by competition with parasitic nestlings (Litovich 1982).

Nesting birds appeared to use several tactics to minimize the cost of parasitism: (1) Eggs were thrown out of the nests if the resident had not begun laying (Stouffer et al. 1987). (2) Incubation was initiated mid-way through laying (Power et al. 1981), most often on Day 3 (Fig. 2). This decreased the amount of time that nests were left unattended, thus making deposition of eggs by parasites more difficult. Alternatively, the incubation behavior of this population may have evolved as a response to the possible benefits of asynchronous hatching (Lack 1954). However, Stouffer (1989)

has shown that both synchronous and asynchronous clutches of the same size fledge the same number of young in this population of starlings. (3) Laying was highly synchronous during early clutches when parasitism was occurring at its highest frequency. Yom-Tov (1975) suggested that synchronous breeding may be the result of conspecific interference during breeding: the more synchronous a population, the less chance that any one bird will experience interference such as parasitism. Parasites will have many nests to parasitize over a short period of time, thus decreasing the probability of parasitizing any one nest. Evans (1988) also reports that early clutches of starlings in England are highly synchronous and experience high frequencies of parasitism. Alternatively, synchrony may simply have reflected a common response to environmental conditions (Dunnet 1955). (4) Hosts laid fewer eggs than they could productively rear in an apparent attempt to avoid having to raise an overcrowded brood in the event that they were parasitized (Power et al. 1989). Thus laying a smaller clutch is a form of "insurance" against the crowding effects of intraspecific brood parasitism.

Parasites may counter host defense tactics by actively searching for unattended nests (Norman and Robertson 1975, Payne 1977). This would account for the difference in time of day that host's and parasite's eggs were laid (Feare et al. 1982).

The lack of synchrony between parasites and hosts was costly to parasites. This was also demonstrated by Evans (1988). The reproductive success of parasites was directly dependent on the time at which their eggs were laid, while the reproductive success of hosts was reduced only by parasitic eggs laid while the host was laying. Parasites probably experienced little benefit (i.e., fledglings) from their parasitism relative to the benefits that they would have experienced had they raised their own clutches. Although the parasitic eggs detected while the host was laying had the same fledging rate as host's eggs, parasites probably laid only one such egg to each host's four or five eggs. But if the alternative to parasitism was to lay no eggs, then a parasitic strategy would be favored. Neither the potential long-term benefits, such as increased longevity by postponing reproduction (Evans 1988), nor the potential long term costs of parasitism could be determined from this study.

No parasite was ever observed laying in a host's nest. However, the identity of parasites falls into two broad categories. First, a parasite may be a female that cannot compete well for nest sites when there are more females than nest sites. This category includes birds that already have nests, but lose them to competitors, and birds that never successfully occupy a nest. The latter includes paired as well as unpaired females. The increase in the number of nest boxes from year to year could have attracted

an overabundance of females in breeding condition. This would account for the relative increase in the cases of parasitism from year to year.

Second, a female could be a parasite and also raise a clutch of her own (Kendra et al. 1988). This behavior could lead to equal or better reproductive success than rearing only a clutch (Brown 1984). This probably did not occur in this population because intermediate and late clutches were not as successful as early clutches. A female parasitizing early clutches, and then laying a clutch of her own later in the breeding season, would be risking total reproductive failure. An adaptive response to this would be to lay an early clutch and then parasitize a later clutch. But there was no evidence for this. Only seven cases of parasitism were detected during later clutches. Perhaps later clutches would always fail if parasitized, eliminating any advantage to parasitism at that time.

Circumstantial evidence leads us to agree with Evans (1988) that parasites were mostly females without nests. Parasitism can probably be maintained in this population at present levels, because an adult starling will usually have more than one opportunity to breed in a lifetime (Coulson 1960, Romagnano 1987). Thus the events of one breeding season do not spell disaster for a female temporarily forced to be a parasite.

In populations where intraspecific brood parasitism occurs at high levels, it is appropriate to ask questions concerning the evolutionary importance of this behavior in shaping the reproductive strategies of those populations. We have attempted to do this by looking at the reproductive success of both hosts and parasites and by observing patterns of behavior. Although it is usually easier to observe hosts, it is necessary to follow parasites so that accurate measures of their reproductive success can be obtained (Emlen and Wrege 1986, Brown and Brown 1989). The consequences of the interactions between hosts and parasites can then be elucidated.

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DIFFERENCES IN TASTE PREFERENCE BETWEEN RED-WINGED BLACKBIRDS AND EUROPEAN STARLINGS

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ABSTRACT.—Consumption of biologically relevant taste stimuli (NaCl, D-fructose, citric acid, tannic acid, L-alanine) by male and female European Starlings (*Sturnus vulgaris*) and male Red-winged Blackbirds (*Agelaius phoeniceus*) were examined in one-bottle tests. Male starlings showed greater avidity for fructose than females, and both males and females exhibited greater avidity for fructose than male Red-winged Blackbirds. In addition, male starlings consumed more citric acid than either female starlings or male Red-winged Blackbirds. For both species, high consumption of NaCl (relative to consumption of other tastes) and low consumption of tannic acid were consistent with data reported for other birds. High consumption of L-alanine by both species (with highest consumption exhibited by male Starlings) suggests sensitivity to and preference for free amino acids. We speculate that one mechanism for inter- and intra-specific differences in food selection under field conditions may be differences in taste sensitivity. *Received 17 July 1989, accepted 20 Sept. 1989.*

Interspecific differences in diet composition among avian species may reflect differences in food preference. In turn, differences in food preference could reflect several factors. For example, there may be interspecific differences in nutritional requirements or metabolic rate. Alternatively, there could be differences in the ability to locate and acquire different food types (Joern 1988). Finally, interspecific differences in taste sensitivity and/or taste preference could influence food selection. The present experiment was designed to assess the latter possibility with Red-winged Blackbirds (*Agelaius phoeniceus*) and European Starlings (*Sturnus vulgaris*). Sex differences in taste preference among starlings was also examined, because this species has been reported to exhibit sexual differences in foraging behavior (Feare 1984).

Red-winged Blackbirds and starlings were chosen for investigation because these species have similar overall feeding strategies. Both consume invertebrates during spring and summer and grains and fruits during fall and winter (Beal 1900, Taitt 1973, Wilson 1978, Feare 1984, Nero 1984). However, there are interspecific differences in overall diet composition. Red-winged Blackbirds are more granivorous than starlings (Harriman 1968, Martinez del Rio et al. 1988). Conversely, starlings consume more

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insects (Bruns and Haberkorn 1960, Martinez del Rio et al. 1988) and more fruit (Harriman 1968, Stevens 1985). If these differences in diet composition are reflected in taste sensitivity, then one might expect starlings to exhibit greater avidity for fructose, citric acid, or free amino acids than Red-winged Blackbirds. Red-winged Blackbirds might show greater tolerance (consumption) of phenolic substances such as tannic acid than starlings.

METHODS

Twenty-five adult male Red-winged Blackbirds and 50 adult starlings (25 males, 25 females) were decoy-trapped in Bowling Green, Kentucky, during October 1986 and shipped to the Monell Chemical Senses Center, Philadelphia, Pennsylvania. Upon arrival, each bird was caged individually (39 × 34 × 61 cm) and visually isolated with pieces of cardboard. Birds were maintained on a 10:14 h light:dark cycle, and water was provided from calibrated 200-ml drinking tubes attached to the center of the front of each cage. Dry food (Purina Flight Bird Conditioner) mixed with oyster shell grit was available ad libitum in food cups on either side of the drinking tubes. After 14 days of adaptation to the laboratory, all birds were placed on a mild water-deprivation schedule that continued for the remainder of the experiment. Deprivation involved removal of the drinking tube during the 14 h dark period of each light cycle. Testing began four days following onset of the water deprivation regime.

Five tastes, each at four different concentrations in aqueous solution, were used: NaCl (0.1%, 0.4%, 0.7%, and 1.0% w/v), D-fructose (0.1%, 0.5%, 1.0%, and 5.0% w/v), citric acid (0.1 mM, 1.0 mM, 0.01 M, 0.1 M), tannic acid (0.5%, 1.0%, 2.5%, and 5.0% w/v), and L-alanine (0.1%, 0.4%, 0.7%, and 1.0% w/v). Also, distilled water was presented as a control. All solutions (except the 5.0% tannic acid solution) were colored brown using McCormick's food coloring (one drop green and four drops red per 300 ml) to match the brown color of the 5.0% tannic acid solution.

Taste stimuli were chosen on the basis of possible biological relevance: all are found in foods consumed by passerines (Goldstein and Swain 1963, Greig-Smith et al. 1983, Wilson and Blunden 1983). Also, tastes were chosen to represent what we presumed to be different taste sensation categories (i.e., salty, sweet, sour, bitter/ astringent, umami [protein taste]). Taste concentrations were selected in part to approximate concentrations present in foods (e.g., concentrations of fructose [0.33 M; Schuler 1983] or citric acid [pH 3.3–4.3; Stevens and deBont 1980] in cherries, concentrations of tannic acid in ash seeds [15–30 mg/g; Greig-Smith 1988]), in part on the basis of work by others (e.g., citric acid, Harriman 1968), and in part on the basis of pilot experiments performed in our laboratory (Espaillat, unpubl. data). These pilot experiments were designed to determine the lowest concentration of tastes that produced reliable differences in consumption relative to consumption of distilled water.

Five Red-winged Blackbirds and 10 starlings (5 males and 5 females) were assigned randomly to each of five groups. Different groups were presented with different taste stimuli (one taste/group) in calibrated 200-ml drinking tubes attached to the center of the front of each cage. Although these one-bottle tests are less sensitive than two-bottle tests in measuring detection, we used the former technique to: (1) eliminate position preferences (Duncan 1960) and (2) assure measurable consumption of unpalatable tastes (e.g., tannic acid). While drinking behavior does not necessarily reflect feeding behavior, we used drinking tests rather than feeding tests to maximize the potential for taste detection. Daily sessions began 1 h after light onset and continued for 2 h on each of 20 successive test days. Measurements of consumption were made at 30-min intervals. The relatively short daily test durations were

chosen to maximize the role of taste (rather than post-ingestional factors) in drinking behavior. No measurements of spillage were made, as we assumed that spillage would be proportional to consumption. Only one stimulus at one concentration was presented daily to each bird. Each concentration (including distilled water as 0.0% taste) of every taste was randomly presented to the birds in the appropriate group four times during the course of testing.

At the end of each test session, stimulus solutions were removed, and birds were permitted free access to distilled water for the remainder of the light period.

Because starlings weigh more than Red-winged Blackbirds, the data were expressed as fluid consumption per g of body mass. Means for the first 30 min of consumption were calculated for the four presentations of each stimulus concentration to each bird and these means were assessed in five two-way analyses of variance (ANOVA, one analysis per taste). The factors in the analyses were sex/species (i.e., male Red-winged Blackbirds, male starlings, female starlings) and concentration (a repeated measures factor). Measurement intervals were not considered as a factor in the analyses because most consumption occurred within the first 30 min of each test session and because patterns in consumption at 60 and 90 min merely reflected those established after 30 min. Tukey Honestly Significant Difference (HSD) tests were used to isolate significant differences among means ($P < 0.05$).

RESULTS

NaCl.—There were no sex/species differences ($P > 0.10$) in consumption of NaCl solutions. However, there were differences in consumption among concentrations ($F = 12.6$; df = 4,48; $P < 0.00001$). Any NaCl solution was preferred to distilled water, and higher NaCl concentrations were preferred to lower concentrations (Fig. 1).

Fructose.—There were significant sex/species differences ($F = 5.1$; df = 2,12; $P < 0.02$). Overall, Red-winged Blackbirds drank less fructose (per gram of body weight) than did starlings, and female starlings drank less fructose did than males. Moreover, post-hoc examination of a significant interaction between sex/species and concentration ($F = 2.6$; df = 8,48; $P < 0.02$) showed that while consumption of fructose by Red-winged Blackbirds did not vary as concentration increased (and at no concentration differed from consumption of distilled water), consumption by starlings did increase (relative to consumption of distilled water) at concentrations $\geq 0.5\%$. Male starlings showed greater consumption of the highest fructose concentration (5.0%) than did females (Fig. 1).

Citric acid.—There were significant sex/species differences ($F = 6.3$; df = 2,12; $P < 0.02$). As for fructose, male starlings consumed more citric acid overall than did either female starlings or male Red-winged Blackbirds. Also, there were significant differences among concentrations ($F = 4.8$; df = 4,48; $P < 0.002$). Post-hoc examination of this effect revealed that cosumption of concentrations ≥ 0.01 M were significantly less than consumption of distilled water (Fig. 1).

Tannin.—There were significant sex/species differences ($F = 7.3$; df = 2,12; $P < 0.01$) and significant differences among concentrations ($F =$

26.5; df = 4,48; $P < 0.00001$). Red-winged Blackbirds consumed more tannin than starlings, but for both species, consumption decreased as tannin concentration increased. Consumption of all tannin concentrations was less than that of distilled water (Fig. 1).

L-alanine.—There were significant differences among concentrations ($F = 6.5$; df = 4,48; $P < 0.0005$). As for NaCl and fructose, consumption increased with concentration (i.e., consumption significantly exceeded that of distilled water at concentrations ≥0.7%). In addition, post-hoc examination of a significant interaction between sex/species and concentration ($F = 4.5$; df = 8,48; $P < 0.01$) showed that both Red-winged Blackbirds and starlings showed increasing consumption with increasing concentration, but male starlings exhibited greater consumption than male Red-winged Blackbirds, and male Red-winged Blackbirds exhibited greater consumption than female starlings (Fig. 1).

DISCUSSION

Both Red-winged Blackbirds and starlings were sensitive to NaCl, fructose, citric acid, tannin and L-alanine. In addition, for fructose, citric acid, and L-alanine, there appeared to be species and sex differences in consumption. While these laboratory results do not necessarily reflect the importance of taste in free-ranging birds, they do provide substance for speculation.

The preference for (i.e., greater consumption of) increasing NaCl concentrations suggests that consumption of salt by free-ranging birds may be mediated by taste (as opposed to post-ingestional feedback). If true, then we speculate that the salt-eating behavior exhibited by a variety of other passerine species (see Coleman et al. 1985 for review) may be taste mediated. Although wild birds rarely show symptoms of sodium deficiency when kept on a low sodium diet (Cade 1964, Dawson et al. 1965), dietary sodium levels of 0.09 to 0.15% are required for maximum growth and egg production (Skadhauge 1981).

The present NaCl results conflict with those reported by Rogers and Maller (1973). Those authors found that Red-winged Blackbirds are indifferent to 0.2% NaCl (relative to water) in 2-bottle tests, yet we observed that 0.1% NaCl was preferred to water in 1-bottle tests. While this discrepancy is probably a function of different experimental designs, a clear explanation is not easily provided. Two-bottle tests are usually more sensitive than 1-bottle tests for evaluation of taste detection (Duncan 1960).

The positive association between fructose consumption and concentration in combination with the negative relationship between citric acid consumption and concentration are consistent with earlier reports (Har-

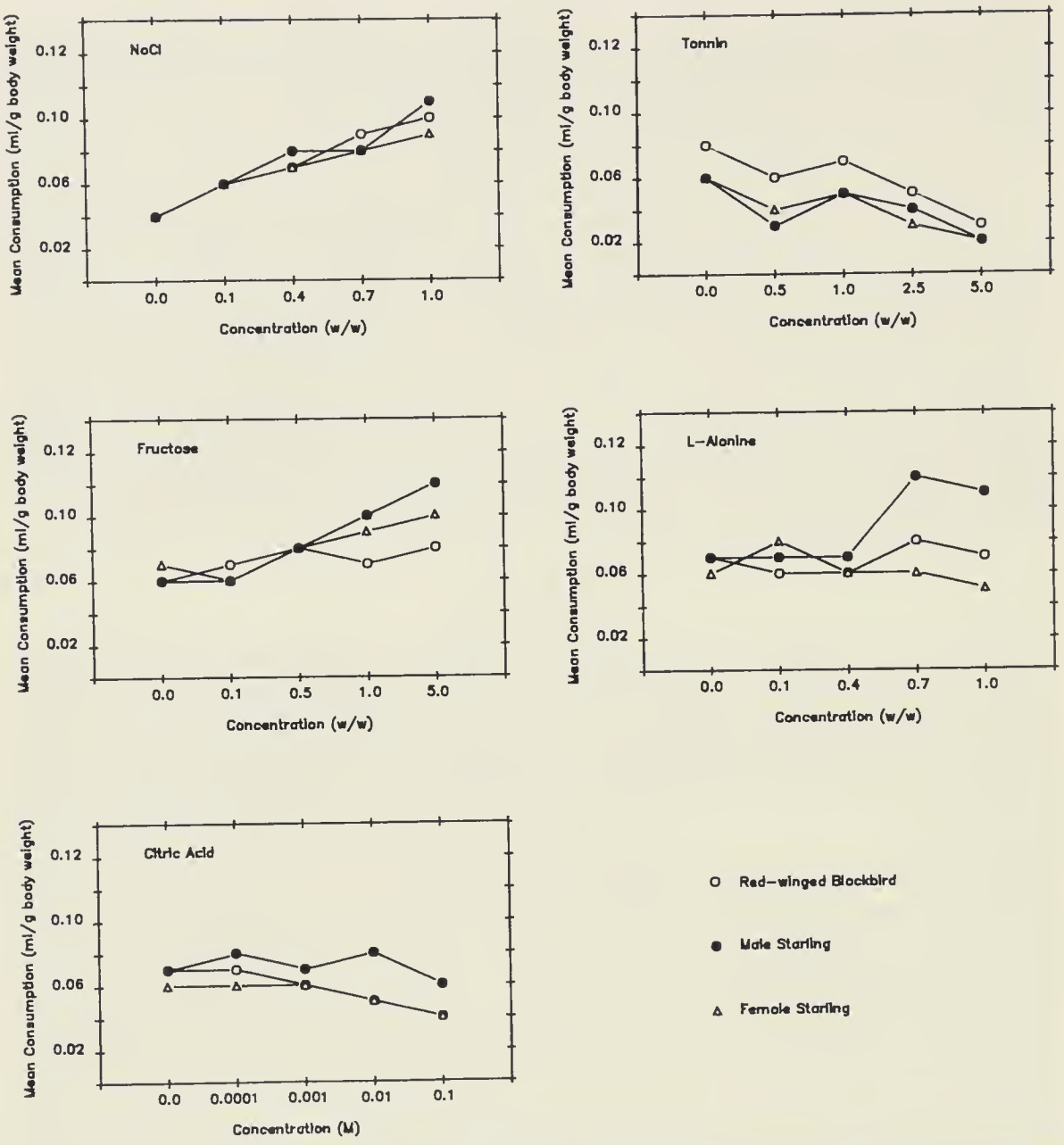

FIG. 1. Mean consumption of NaCl, fructose, citric acid, tannin, and L-alanine per gram of body weight by Red-winged Blackbirds, male starlings, and female starlings.

riman 1968, Martinez del Rio et al. 1988, Martinez del Rio and Stevens 1989). Because the pulp of many fruits is rich in both substances, it is reasonable to speculate that preference for fructose and preference for or tolerance of citric acid represent sensory adaptations to frugivory. The fact that starlings consumed more fructose and citric acid than Red-winged Blackbirds is consistent with this view, insofar as the former species eats relatively more fruit (e.g., Harriman 1968).

Tannic acid concentrations tested in the present experiment are equivalent to those found in various fruits (Goldstein and Swain 1963) and

grain (Bullard et al. 1981). The finding that consumption decreased with increasing concentration for both species is consistent with data which show that the tannin content of fruits and grain is positively correlated with bird resistance (e.g., Bullard et al. 1981, Greig-Smith et al. 1983, Mason et al. 1984). That Red-winged Blackbirds were more tolerant than starlings of low (0.5–1.0%) tannin concentrations may reflect their granivorous feeding habits (i.e., Red-winged Blackbirds may be more likely to utilize tannin-containing foods).

We cannot explain our observation that both male starlings and Red-winged Blackbirds show greater consumption of L-alanine than female starlings. However, the more general finding that both species are sensitive to and prefer this amino acid at concentrations $\geq 0.7\%$ is intriguing. Whether or not L-alanine sensitivity reflects sensitivity to other free amino acids or to protein is unknown. However, L-alanine and similar substances (e.g., L-glutamine) occur as free amino acids in both vegetable matter, fruit, and meats (Hac et al. 1949, Maeda et al. 1958, Baker and Baker 1983). Perhaps amino acid sensitivity aids in the identification of high protein foods. At least for starlings, assimilation efficiency increases as the protein content of a diet increases (Twedt 1984).

Overall, the present findings implicate chemosensory cues as one of the factors involved in foraging decisions. This possibility stands in contrast to models of foraging (e.g., Wunderlee and Cotto-Navarro 1988) that mainly or only consider energy (i.e., long-term physiological feedback) as a proximal determinant. Taste cues may provide an immediate sensory signal concerning the quality of a potential food item, thereby maximizing foraging efficiency.

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CHOICES OF FEEDING HABITAT BY RELICT MONTEZUMA QUAIL IN CENTRAL TEXAS

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ABSTRACT.—Montezuma Quail (*Cyrtonyx montezumae*) were studied at the eastern edge of their range on the Edwards Plateau, Texas. Population densities were similar on a moderately grazed and an ungrazed ranch. Feeding habitat, revealed by holes dug for wood sorrels (*Oxalis drummondii*) and the discarded sorrel hulls, was compared to concurrently unused habitat containing the sorrels but no holes and hulls. Significantly different means and reduced variation in the chosen habitat features were considered criteria of habitat selection. The quail chose feeding sites primarily on the basis of tall-grass (hiding) cover but also chose deep, dry soils on slopes in relatively open Madrean evergreen woodland. Tall-grass cover predicted the location of feeding sites most often on the grazed ranch, where that cover-type was patchier. When grazing removes 40–50% of the tall grasses in an area, we believe the quail are extirpated (a nearby, formerly occupied, overgrazed site had only 25% tall-grass cover). *Received 3 Feb. 1989, accepted 9 Oct. 1989.*

Montezuma Quail (*Cyrtonyx montezumae*) inhabit open, evergreen woodlands in Mexico and the Southwest, including isolated areas in central and Trans-Pecos Texas. The species was studied in southern Arizona (Wallmo 1954; Marshall 1957; Bishop and Hungerford 1965; Brown 1976, 1978, 1982) and Chihuahua, Mexico (Leopold and McCabe 1957) but is poorly known in Texas (Fuertes 1903), where it has declined in numbers and range over the past century (Oberholser 1974, Gehlbach 1981). Originally, Montezuma Quail ranged across the southern Edwards Plateau, Texas, into the Trans-Pecos, but native birds are now very local (Sorola 1986) and on one endangered species list (Texas Organization for Endangered Species 1988).

Leopold and McCabe (1957) observed that the birds declined when overgrazing destroyed their food supply, although Brown (1978, 1982) noted that heavy grazing increased food but still caused a decline in the quail, because escape or hiding cover was reduced. The removal of most available forage grasses eliminated Montezuma Quail locally in southern Arizona (Brown 1982). Major plant foods and escape cover were coextensive in Texas, so overgrazing might have destroyed both features (Gehlbach 1981).

Montezuma Quail dig the bulbs of sedges (*Cyperus*) and wood sorrels

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(*Oxalis*) in Arizona (Bishop and Hungerford 1965; Brown 1978, 1982), Chihuahua (Leopold and McCabe 1957), and Texas (pers. obs.). Upon excavating these major foods, the birds eat fleshy portions, leaving hulls in or near a small hole (Leopold and McCabe 1957, Bishop and Hungerford 1965, Brown 1978). This sign of feeding may be used for census purposes (Brown 1976), and by contrast to nearby areas without fresh holes, as an indicator of habitat choice.

Despite continued grazing, Montezuma Quail persist in the Rocksprings area of the Edwards Plateau. This is not general knowledge (cf. Johnsgard 1973, Oberholser 1974, Sorola 1986), and there is no quantitative study of the species or its environment in Texas. We observed birds and their choices of feeding habitat at two Edwards Plateau ranches, employing principles of investigation and data analysis similar to McCallum and Gehlbach (1988). We tested the null hypothesis that Montezuma Quail feed indiscriminately throughout occupied habitat and used the results of this study to appraise a formerly occupied and apparently overgrazed locale.

STUDY SITES

The ranches (17 km SW Rocksprings, Edwards County, 500 m) were a sheep-goat-cattle operation, about 10 ha/animal unit, and a deer and turkey-hunting reserve ungrazed by domestic livestock for four years. At each ranch, we located a 25-ha study site inhabited by Montezuma Quail year-round. These sites had similar populations as judged from quail flushed during habitat assessments in September 1981 through July 1982 (mean = 0.08 ± 0.05 [SD] and 0.10 ± 0.07 birds/ha, respectively, N = 13 each, Wilcoxon $P > 0.50$). However, we could not account for repeated observations of the same birds. Northern Bobwhites (*Colinus virginianus*) were present in similar numbers (0.18 ± 0.10 birds/ha, Wilcoxon $P = 0.43$).

A brushy, evergreen woodland of 521 stems/ha, dominated by *Quercus fusiformis, Diospyros texana, Rhus virens,* and *Sophora secundiflora,* characterized the grazed ranch. *Q. fusiformis, D. texana,* and *Berberis trifoliolata* dominated the more open, evergreen woodland of 140 stems/ha on the ungrazed ranch. Dominant tall grasses at both sites were *Aristida wrightii,* and *Bouteloua curtipendula,* followed by *Schizachyrium scoparium.* Short grasses were primarily *Hilaria belangeri* in the open and *Stipa leucotricha* under woody cover and grew on flats by contrast to tall grasses on the slopes. *Juniperus ashei* and *Pinus cembroides* were present on both ranches, adding to the general aspect of Madrean evergreen woodland (Amos and Gehlbach 1988).

Kickapoo Caverns State Park (50 km SW of Rocksprings, Edwards-Kinney counties, 550 m) was our third site, studied in March and September 1988. Montezuma Quail were present historically (S. Sorola, pers. comm.) but absent during the study (they were found only 1 km away). This park had been a sheep-goat-cattle ranch but was ungrazed one year before sampling. Its evergreen woodland of 312 stems/ha was dominated by *Q. fusiformis* and *D. texana,* as well as *J. ashei* and *P. cembroides. B. trifoliolata* and *Karwinskia humboldtiana* were the leading shrubs; *A. wrightii* and *H. belangeri* were the most important tall and short grasses, respectively.

Because Montezuma Quail habitat elsewhere is at least 500 m higher in elevation, drier,

and has a July-September rainfall pattern (monsoon) that triggers nesting (Leopold and McCabe 1957), we noted climatic and reproductive differences at the species' eastern edge of range on the Edwards Plateau. In our study, area mean annual rainfall is 54 cm, but as much falls in April–June (33%, mean temperature = 24°C) as in July–September (35%, 28°C; Larkin and Bomar 1983). We found hatchlings on June 15th, and young birds were about half-grown on September 18th, suggesting late summer nesting as well.

METHODS

On the ranches, two perpendicular 10-m line-intercept transects measured ground cover at each feeding place, indicated by a concentration of recently dug holes and associated bulb hulls of the wood sorrel (*Oxalis drummondii*) (=chosen habitat). Vegetation included seven categories: tall grass (>0.3 m), short grass (<0.3 m), oak-leaf litter, other-leaf litter, erect forbs, prostrate forbs, and dead wood (sticks, logs, bark). Physical cover was either Edwards limestone outcrops or bare soil, sometimes with a partial cover of *Selaginella* sp.

At each transect intersection, we measured the distance to and canopy diameter of the nearest tree (lowest limbs above 0.3 m) and shrub (limbs below 0.3 m) in each of the four quarters and synthesized the data per stratum (Cottam and Curtis 1956). Also measured at the intersection were slope angle, site exposure (N = 1, NE = 2, E = 3, etc.), and soil depth, plus temperature and moisture at average bulb depth (=5 cm; *O. drummondii* was not visible above ground all year, hence could not be measured directly). Each variable was a known or potential aspect of food or shelter based on the literature, a week of pre-study observations, and general experience (Gehlbach 1981).

After each feeding habitat sample was taken, concurrently unused habitat was selected randomly within 100 m and assayed in the same manner. This habitat lacked holes and hulls but had *O. drummondii,* at least in the fall when the wood sorrel was most evident. A thorough search for signs of recent feeding within 10 m of each transect assured veracity of the sample, and all feeding and unused samples were marked to avoid resampling. We emphasize that we studied choice of feeding habitat rather than habitat versus non-habitat, because Montezuma Quail were seen at or near both feeding and unused sites on both ranches.

Samples were taken monthly in March–May (spring, quail paired and calling), June–July (summer, hatchlings found), September–November (fall, half-grown birds), and December–February (winter, coveys). The data were analyzed by season as well as by site, because we anticipated changing demands by the birds and vegetational differences related to season in addition to feeding preferences related to grazing impact and landscape variation.

Analyses of variance (ANOVAs) of all 18 physical and biotic parameters, arcsine or log-transformed as necessary, tested mean differences between the ranches, seasons, and habitats. Significant ($P = 0.05$) parameters were then employed in multiple stepwise regressions (MSRs) to reveal the amount of variation in feeding versus unused habitat determined by each parameter simultaneously. Habitat choices are also shown by reduced variation in the data from used sites (Ratti et al. 1984), and degree of selectivity is indicated by the amount of variance reduction (McCallum and Gehlbach 1988). Thus, we calculated coefficients of variation (CVs) of the significant parameters and used two-tailed Wilcoxon signed-ranks tests of the CVs to evaluate the postulated differences in variation.

Only those variables that significantly described feeding habitat at both ranches in the spring and fall were measured at Kickapoo Caverns State Park. They were soil depth, oak-leaf litter, other-leaf litter, tall-grass, and shrub cover. Field methods were the same except that 30 random samples of potential feeding habitat were taken over 25 ha. Potential feeding habitat was defined from the ranch study as having tall grasses and wood sorrels. Since we

hypothesized that the park and ranch feeding habitats were the same, we compared them with ANOVAs of the five indicator variables.

RESULTS

Ranches.—The grazed and ungrazed ranches differed according to 13 of the 18 habitat parameters. For example, the grazed site had greater slope, tree density, and more bare ground (highest F-values). Of special importance, however, are variables that were the same at both ranches (exposure, soil depth and moisture, tall- and short-grass cover), because all except exposure were important distinguishing features of feeding habitat.

At the grazed ranch, feeding and unused habitats were distinct all year; 10 of the 18 parameters were significantly different. Tall- and short-grass cover (both greater in feeding habitat), tree density, soil moisture, and shrub cover (less in feeding habitat) had the highest F-values. This result was the first of six instances among 10 inter-habitat comparisons on both ranches in which tall-grass cover was a significant predictor of habitat choice (Table 1).

Feeding and unused habitats also were discernible year-round at the ungrazed ranch. Significant differences were discovered in soil depth, soil moisture, and tall-grass cover. Soil depth and tall-grass cover were greater, and soil moisture less, in the chosen feeding areas (Table 1). Among the four features involved in distinguishing habitats at both ranches, listed above, all showed smaller mean differences at the ungrazed site, suggesting more continuous habitat (less patchiness) and hence less discrimination by Montezuma Quail.

Nevertheless, the birds were selective as revealed by the smaller CVs of environmental features that significantly predicted feeding habitat (Table 1). On the ungrazed ranch year-round, CVs of all significant features averaged 40% in feeding areas compared to 58% in unused habitat (Wilcoxon $P = 0.03$). Apparently even more selectivity prevailed on the grazed ranch ($\bar{x}$ CVs = 31% vs 50% in unused habitat, $P = 0.01$), but there was no inter-ranch difference in the reduced habitat variation associated with feeding ($P = 0.25$).

Seasons.—Significant differences among the four seasons were apparent in 10 of the 18 parameters on both ranches. The three soil features had the highest F-values. Among vegetational variables which we thought might change seasonally, both types of grass cover, other-leaf litter, and erect-forb cover increased significantly from spring into fall. Total variation explained by the MSRs was considerable in summer (R^2 = 81% grazed, 97% ungrazed) and fall (R^2 = 72% grazed, 73% ungrazed) but dropped in winter (48%, 33%) and spring (39%, 22%), possibly because

TABLE 1

ENVIRONMENTAL FEATURES THAT PREDICT DIFFERENCES IN FEEDING HABITAT COMPARED TO HABITAT CONCURRENTLY UNUSED FOR FEEDING BY MONTEZUMA QUAIL[a]

	Grazed ranch				Ungrazed ranch		
	r^2 added	Feeding habitat	Unused habitat		r^2 added	Feeding habitat	Unused habitat
All-Year (N = 78 grazed, 68 ungrazed)							
Tall-grass cover (m)	0.34	13.2, 37%	6.9, 58%	Soil depth (cm)	0.18	8.3, 29%	6.4, 59%
Short-grass cover (m)	0.08	10.0, 74%	3.2, 75%	Soil moisture (%)	0.06	13.2, 35%	24.5, 56%
Tree density (N/ha)	0.03	173.0, 44%	314.0, 62%	Tall-grass cover (m)	0.05	13.0, 53%	9.3, 77%
Spring (N = 20 grazed, 20 ungrazed)							
Soil depth (cm)	0.39	8.9, 10%	6.2, 37%	Slope (°)	0.22	3.6, 46%	1.6, 75%
Summer (N = 14 grazed, 12 ungrazed)							
Shrub density (N/ha)	0.44	318.0, 22%	789.0, 39%	Slope (°)	0.76	2.3, 21%	5.7, 25%
Tall-grass cover (m)	0.37	16.2, 33%	10.3, 42%	Rock cover (m)	0.19	17.5, 25%	34.4, 26%
				Tall-grass cover (m)	0.02	16.8, 10%	9.2, 49%
Fall (N = 20 grazed, 14 ungrazed)							
Tall-grass cover (m)	0.43	13.3, 41%	5.6, 66%	Soil moisture (%)	0.73	14.3, 34%	77.2, 37%
Short-grass cover (m)	0.29	9.9, 72%	2.5, 76%				
Winter (N = 24 grazed, 22 ungrazed)							
Tall-grass cover (m)	0.48	11.9, 29%	5.4, 67%	Soil depth (cm)	0.33	8.4, 23%	5.3, 46%

[a] Features are listed in order of their explanation of significant ($P = 0.05$) variational differences between the two habitat-types on each ranch (r^2 additions to R^2 in one all-year and four seasonal multiple stepwise regressions per ranch). Means and coefficients of variation (%) are given.

unmeasured factors became more important relative to the seasonally reduced, herbaceous vegetation (Table 1).

Comparing habitats at the two ranches in spring, we found few similarities. The quail chose feeding areas with greater soil depth, more tall grasses, and fewer trees on the grazed ranch but greater slope and more dead wood, erect forbs, and shrub cover on the ungrazed ranch. Soil depth (grazed) and slope (ungrazed) were the only significant predictors (Table 1), but all indicators were significantly less variable among samples of feeding habitat on the two ranches combined. Thus, the birds were selective seasonally ($\bar{x}$ CVs = 55% vs 97% in unused habitat, Wilcoxon $P = 0.04$).

More tall-grass cover predicted feeding habitat on both ranches in the summer, with other significant determinants being lower shrub density (grazed) and less slope and rock cover (ungrazed, Table 1). Not only was variation among the habitat factors significantly reduced in the summer feeding areas of both ranches ($\bar{x}$ CVs = 30% vs 56% in unused habitat, Wilcoxon $P = 0.01$), it was reduced compared to feeding habitat in the spring ($P = 0.05$). This suggests even more rigorous selectivity.

By fall more tall- and short-grass cover, less soil moisture, and lower shrub density indicated feeding habitat on the grazed ranch. Less moisture and lower tree density characterized feeding areas on the ungrazed ranch, but significant predictors were the grasses and moisture (Table 1). Similarly, in winter the tall grasses indicated feeding habitat only on the grazed ranch, along with greater slope and soil depth. The latter also predicted chosen areas on the ungrazed site. Variation of both the selected and unused habitats decreased from fall to winter, although significant within-season differences remained ($\bar{x}$ CVs = 45% vs 67% in fall and 29% vs 47% in winter, Wilcoxon $P = 0.05$).

Tall-grass cover.—This most frequently identified variable predicted feeding habitat in three seasons at the grazed ranch but only during summer at the ungrazed ranch (Table 1). By adding significant r^2 values of variables in four seasonal MSRs per ranch and comparing hierarchies of the sums of those variables in common, we found that tall-grass coverage ranked first at the grazed site and last at the ungrazed ranch (Table 2). The order of parameter influence on habitat choice was reversed ($r_s = -0.90$, $P = 0.03$). Vegetation was more important in the presence of livestock, whereas physical factors prevailed in their absence (Table 2).

State park.—The Kickapoo Caverns State Park site was quite distinct from both ranches, since four of the five indicator variables were different (Table 3). Tall-grass cover was 60% less extensive, and shrub cover 58% greater, while the leaf litter was 123–203% greater in contrast to the feeding habitat on both ranches. This suggests that the park area had been overgrazed and was unsuitable for the quail.

TABLE 2

HEIRARCHY OF ENVIRONMENTAL FEATURES, COMMON TO BOTH RANCHES, THAT EXPLAIN DIFFERENCES IN FEEDING HABITAT COMPARED TO HABITAT CONCURRENTLY UNUSED FOR FEEDING BY MONTEZUMA QUAIL

Features (in feeding habitat)	Grazed ranch	Ungrazed ranch
Tall-grass cover (more)	1.28	0.02
Shrub density (less)	0.44	0.08
Soil depth (more)	0.39	0.34
Soil moisture (less)	0.01	0.73
Slope (more)	0.06	0.97

[a] Values are the sums of significant ($P = 0.05$) r^2 additions to R^2 from four seasonal multiple stepwise regressions per ranch.

DISCUSSION

Relict Montezuma Quail persist on the Edwards Plateau, Texas. There, population densities are similar on moderately grazed and ungrazed sites ($\bar{x} = 0.09$ birds/ha). They are also similar to densities in Arizona (0.08–0.9 birds/ha; Brown 1978, 1982; Gehlbach unpubl.) and Chihuahua (0.1 birds/ha, Leopold and McCabe 1957). It appears that grass cover taller than 0.3 m is the most critical component of feeding habitat on the plateau, particularly on grazed land. Whereas tall grasses were implicated 60% of the time in our analyses of feeding sites, short grasses were involved only 20% of the time and not at all on ungrazed land (Tables 1 and 2).

As significant predictors of feeding habitat, tall grasses constituted 70 ± 10% ($\bar{x}$ ± SD) of ground cover compared to 39 ± 11% in habitat unused for feeding (N = 6 each from Table 1). Formerly occupied overgrazed land averaged only 25% tall grass cover, following a year of no grazing, but occupied habitat averaged 62% (Table 3). Brown (1982) found that most Montezuma Quail in southern Arizona inhabited areas having average livestock utilization levels below 46% and suggested that grazing 46–50% of the grasses produced marginal conditions. If our coverages are roughly comparable, then the chosen tall-grass habitat in central Texas is only 20–40% grazed, whereas unused habitat is marginal to unsuitable (50–72% grazed).

Our grazed and ungrazed sites had similar tall- and short-grass cover, but tall grasses were more important to Montezuma Quail on the grazed site, where they were patchier and hence scarcer. Also, the birds choose relatively open ground on the more densely wooded, grazed land. Apparently, if tall grasses are sufficient but quite patchy with respect to dense woody vegetation, a common result of grazing (Amos and Gehlbach 1988), then more grass and fewer woody plants both predict feeding habitat

TABLE 3

POTENTIAL MONTEZUMA QUAIL FEEDING HABITAT AT KICKAPOO CAVERNS STATE PARK (OVERGRAZED, FORMERLY INHABITED BY THE BIRDS) COMPARED TO ACTUAL FEEDING HABITAT AT GRAZED AND UNGRAZED RANCHES NEARBY[a]

Feature	*F* (*P*)	State park (N = 30)	Ranches (N = 37)
Shrub cover (m)	8.3 (<0.001)	12.2, 51%	7.7, 47%
Tall-grass cover (m)	7.7 (<0.001)	5.0, 44%	12.4, 43%
Oak-leaf litter (m)	3.7 (=0.01)	10.3, 107%	3.4, 136%
Other-leaf litter (m)	2.6 (=0.04)	13.4, 92%	6.0, 91%
Soil depth (cm)	1.8 (NS)	6.5, 52%	8.2, 28%

[a] Data are means and coefficients of variation (%).

(Table 2). Perhaps there is a trade-off between the two cover-types favoring tall grasses, the more important habitat predictor, because we saw the quail take refuge in both kinds of cover but did not find feeding habitat beneath a woody canopy.

In the absence of grazing and hence presence of more continuous grass cover, tall grasses were still important year-round but particularly in summer when feeding site selection was especially rigorous. Deeper, drier soils also were critical (on the grazed land too, Table 1). We think the quail choose such soils, because we observed more wood sorrels growing in deeper soils and found their bulbs easier to dig under drier conditions. Presumably the birds are similarly constrained. Slope also emerged as a major indicator of feeding habitat on the flatter, ungrazed study site (Table 2). In spring, when rainfall is considerable, the quail choose steeper slopes that should be relatively drier because of increased runoff. But in summer they choose flatter places, since bulbs give way to insects as primary foods (Bishop and Hungerford 1965, Brown 1982), and digging apparently is not as frequent (Table 1).

The link between overgrazing and decline of Montezuma Quail has been surmised since the 1920s (Leopold and McCabe 1957) but only recently quantified (Brown 1982). We refine that link by showing reduced tall grasses and increased shrubs in potential feeding habitat at a formerly occupied locale. For the first time we demonstrate that the quail choose certain sites on the basis of hiding cover over others with presumably similar food potential. These sites have mostly tall-grasses on slopes with deep, dry soils in an evergreen woodland matrix. We suggest that both the required habitat, and thus the quail, are dispersed patchily in response to natural landscape heterogeneity and grazing impact. We postulate that grazing increases the patchiness, eventually eliminating the quail when 40–50% of the tall-grass (hiding) cover is removed.

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SHORT COMMUNICATIONS

Introduced and invading birds in Belém, Brazil.—The region of the Brazilian Amazon port city of Belém Pará (Fig. 1), has undergone rapid change while the human population has grown from less than 300,000 in 1950 to over 1,000,000 in 1988. Once set in a landscape dominated by tropical rain forest, Belém today is a patchwork of residential areas, second-growth on both dry and flooded sites, industrial installations, and artificially maintained grassland. Only small patches of the original forest remain. Here we report on the status and distribution of six species of birds that have been introduced to Belém by man or have expanded their ranges to take advantage of habitat alteration. Introductions and range expansions can be viewed as opportunities for studying changes in community structure. In addition to the species treated below, the Budgerigar (*Melopsittacus undulatus*) and the White-throated Seedeater (*Sporophila albogularis*) have been introduced repeatedly as escaped cage birds in Belém in recent years, but apparently without becoming established.

Jandaya Parakeet (*Aratinga solstitialis jandaya*).—This parakeet has for a long time been reported as occurring in northeastern Brazil from Maranhão and the north of Goiás to the northern limits of Bahia (Pinto 1938, 1978; Forshaw 1978). Goeldi's (1894) old sight record of the species on the northern coast of the state of Pará has been ignored. More recently we have recorded it in inland eastern Pará near the Maranhão border and the Serra dos Carajás. The Jandaya Parakeet was first reported for Belém by Ridgely (1982), based on observations by Oatman. The Museu Goeldi houses a specimen (MPEG 35, 357) of a molting adult male with testes 3 × 2 mm collected in the Belém district of the Marambaia on 27 Apr. 1982. We estimated the Belém population of the Jandaya Parakeet at approximately 50 individuals in 1984, and it has since more than doubled. The species inhabits 2–10-m-high second-growth which is abundant at the periphery of the city. During our observations, the birds fed principally on fruits of certain Melastomataceae, mango (*Mangifera indica,* Anacardiaceae), caranã (*Mauritia huebneri,* Palmae), and various species of cecropia (*Cecropia* spp., Moraceae). Maize (*Zea mays*) and rice (*Oryza* spp.) from fields along the main roads that lead to Belém are also important components of the diet of this parakeet. They were nesting in pairs using natural and woodpecker-made hollows in trees at least 15 m tall. The reproductive season extends from August to December. In 1983 approximately eight pairs nested in an area of flooded second-growth in Marambaia. The distance between nests was about 50 m. No intraspecific aggression was observed, and individuals nesting in one cavity frequently landed on other pairs' nest trees and entered their nest cavities, especially early in the reproductive cycle. Between 55 and 60 days (average 58 days) elapsed between nest preparation and fledging of the young. The fledglings (one or two per nesting pair) were smaller and much greener than adults.

These parakeets moved and changed habitat preferences seasonally. In Marambaia the birds appeared sporadically from March through July, and then appeared regularly in numbers and reproduced in the flooded second-growth, followed by disappearance of the flocks and sporadic occurrence again. The origin of the Belém population of Jandaya Parakeets can be attributed to human influence. The vegetation that has replaced the original rain forest in most of the Belém district east to the border with Maranhão is readily colonized by the species. Commercial traders in live birds have probably had an important role in the dissemination of Jandayas as well. The Belém animal market traditionally has received large numbers of live birds from Ceará and Maranhão, including many Jandaya Parakeets. The latter are extraordinarily raucous, chew their cages aggressively, and often are liberated intentionally or escape to form colonizing populations (Oren and Novaes 1986). We consider the population of *A. s. jandaya* in Belém as established and expanding.

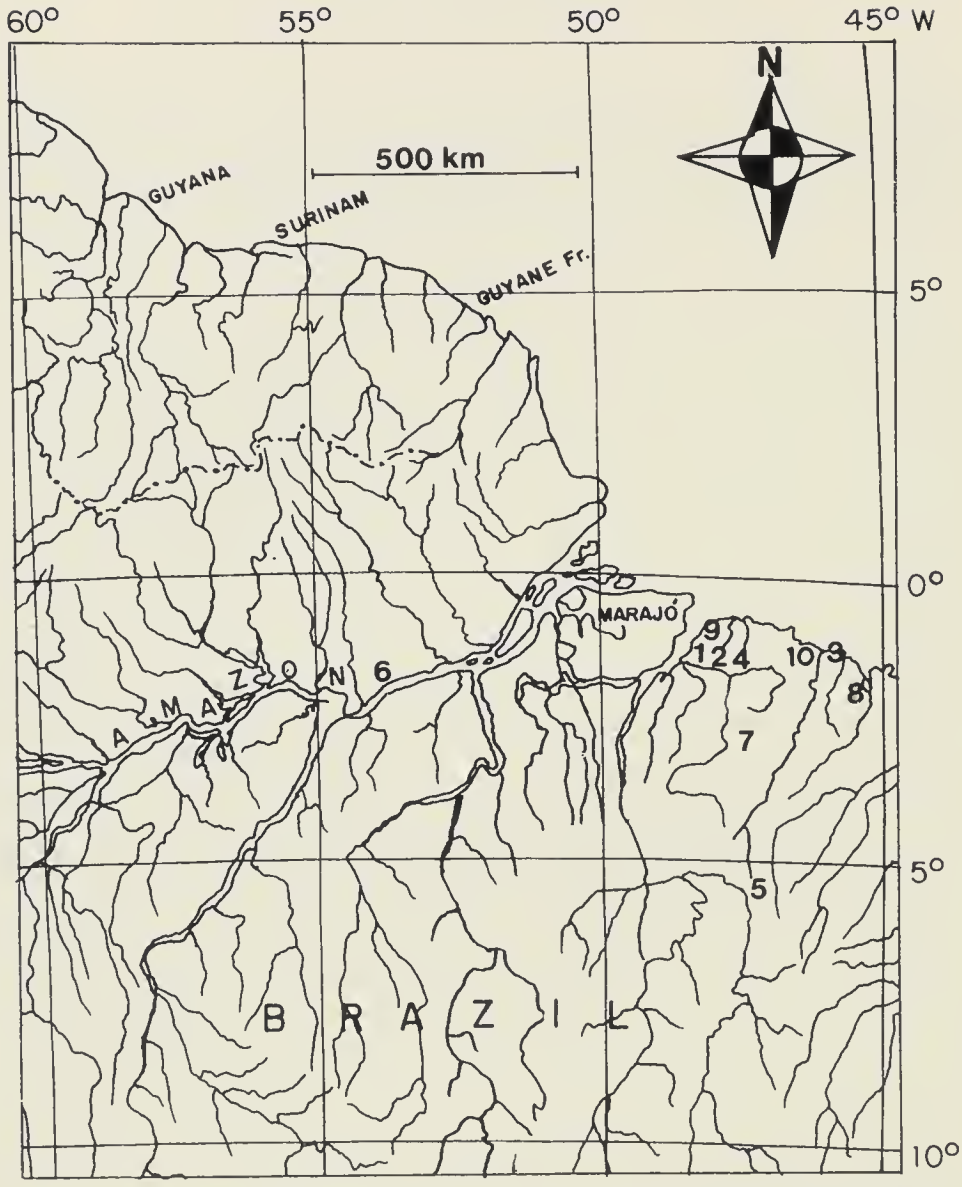

FIG. 1 Map of northeastern South America. Numbers indicate the following localities: (1) Belém; (2) Benevides; (3) Carutapera; (4) Castanhal; (5) Imperatriz; (6) Monte Alegre; (7) Paragominas; (8) Turiaçu; (9) Vigia; (10) Bragança.

Guira Cuckoo (*Guira guira*).—Before 1982, the Guira Cuckoo was not recorded in Belém. Now it is found in open fields and pastures near Tenoné and the extensive lawns of the Federal University of Pará (UFPa) and the Faculty of Agricultural Sciences (FCAP) in the district of Guamá. Approximately 60 individuals were resident in 1985 at the park-like habitat of the two universities. This population diminished in the rainy season (Jan.–Apr.), when flocks were small and scattered and had entered the second-growth bordering the lawns. In April the birds all returned to the lawns in flocks of up to 15 individuals. The birds fed (N = 200 observations) either on the ground (75% of observations) or the tops of trees and shrubs (25%). The diet consisted mostly of arthropods (especially Orthoptera), lizards (*Tropidurus* sp.) and frogs (*Hyla* sp.). We found communal nests in September (1), October (3), and November (1), 1984. The irregularly rounded nests, similar to those previously reported for the species (Davis 1940), were placed at the petiole bases of palm leaves 1.8–8.0 m above the ground. The November nest held 12 eggs. Since these first observations,

the Guira Cuckoo has expanded its population and spread to additional sites in the Belém region, and in 1988 it was commonly observed in open habitats.

Considering the extensive ornithological exploration of the region in the past and the conspicuousness of the Guira Cuckoo, it is clear that this species is a recent arrival in Belém that has colonized man-made habitat. The closest historical records for *G. guira* to Belém are Marajó Island and Bragança (Snethlage 1914, Pinto 1938, Novaes and Pimentel 1973), both of which are regions of extensive natural grasslands. The Guira Cuckoo has the habit of making long "kiting" flights using the wind (Sick 1985). The prevailing winds in Belém most of the year are from the NNE (Penteado 1968), favoring a Marajó origin for the Belém population. Such a hypothesis is further strengthened by the appearance of one Gray Monjita (*Xolmis cinerea*) at the Federal University campus in 1984, three Toco Toucans (*Ramphastos toco*) near Tenoné in July 1988, and five Peach-fronted Parakeets (*Aratinga aurea*) at the research campus of the Museu Goeldi in Jan. and Feb. 1989, all species most certainly vagrants from Marajó. There are no records for *G. quira* in areas of appropriate habitat between Belém and Bragança, making it unlikely that the Belém population was formed by individuals from the east.

Troupial (*Icterus icterus*).—Two distinct forms of *Icterus icterus* occur around Belém: *I. i. jamacaii,* with a black head, recorded from Maranhão through northeastern Brazil to Minas Gerais (Pinto 1944); and *I. i. croconotus,* with an orange head, distributed in the Amazon basin from Ecuador, Peru, and Bolivia to Guyana, Mato Grosso and western Pará (Pinto 1944, Blake 1968). The specimen records closest to Belém are Imperatriz, Maranhão (*I. i. jamacaii*) and Montc Alegre (*I. i. croconotus*), and *I. i. croconotus* is common in the delta region of the lower Amazon (Oren, pers. obs.). Our recent (1980–88) sight records of *I. i. jamacaii* from Turiaçu, Carutapera, Vigia, Benevides, Paragominas, and Castanhal suggest a natural westward expansion of the race. The earliest sight record for Belém is from 1981, since which date the bird has become increasingly common in the city. This subspecies of Troupial is also common in the live bird market, so escape from captivity probably has accelerated the natural range expansion already underway. The other subspecies, *I. i. croconotus,* was probably introduced to Belém as a cage bird. Although illegal, live bird commerce from the lower Amazon to Belém continues on a significant scale, and birds of this race are among the most valuable and sought-after. Both races can be found in Belém in second-growth woods and isolated trees with edible fruit. *I. i. jamacaii* is much more common than *I. i. croconotus,* and is usually found in pairs, whereas most observations of *I. i. croconotus* are of single individuals. The feral Troupials in Belém are extensively hunted by local people for the cage bird trade. Contact of these two distinctive forms in Belém should help establish whether they should be classified as separate species, or retained as subspecies of the same biological species; the latter treatment is followed by most recent authors.

Red-cowled Cardinal (*Paroaria dominicana*).—This is another species brought to Belém by the commercial trade in live birds. It is common in captivity in northeastern Brazil, its presumed point of origin, and is common in the market of Belém, more for its colorful plumage than its song. We have scattered records (1983–88) from various districts of urban Belém (Marco, Telégrafo, Marambaia, Nazaré, Praça da República) of groups of 2–5 individuals. Most of these records are from areas of intense human traffic and were probably recent escapes from captivity. We have no evidence of breeding.

House Sparrow (*Passer domesticus*).—The House Sparrow was introduced to Brazil at Rio de Janeiro at the beginning of this century (Sick 1959). Subsequent introductions and natural expansion of established populations have spread the species widely in Brazil. *Passer domesticus* was introduced in Belém between 1925 and 1927, but the small flock from Rio de Janeiro quickly died out; Sick (1959) hypothesized that problems in adapting to the wet Belém climate were important in the introduction's failure. In the 1960s feral populations

of House Sparrows began to appear in Brazilian Amazonia, advancing along new highways (Müller 1967, Smith 1973) and along the coast (Smith 1980). The species was first noted in Belém in 1978 and has since increased in abundance and distribution in the city. It is essentially an urban bird, common in the port dock area, city squares, and gasoline stations. The birds have not been recorded in two large wooded, urban parks (Museu Paraense Emilio Goeldi and Bosque Rodrigues Alves), nor do they enter native second-growth. The three districts where the birds are most common (Cidade Velha, Comércio, and Icoaraci) are undergoing rapid architectural modification, but they still have an abundance of old houses with eaves and cavities used for nesting. In the rest of the city, the flocks of *P. domesticus* are small (≤six individuals) and scattered, and the birds are notably shy, avoiding the approach of people. Nesting was observed almost year round with the following records: Feb. (3 nests), Mar. (5), May (2), July (2), Oct. (3), Nov. (1), and Dec. (2). Nests were in eaves and roof cavities and even traffic lights. The birds foraged on the ground among foliage or rarely made short flights after alate termites and other small arthropods. They fed on a wide variety of foods, including popcorn, nematodes, insects, flowers, fruits, and grass seeds. The Belém population of House Sparrow is well-established and expanding. The current population distributed throughout the urban zone is estimated at around 1000 individuals.

Common Waxbill (*Estrilda astrild*).—The Common Waxbill was introduced to Brazil at Rio de Janeiro in the last century (Santos 1948; Sick 1968, 1985). Since then the species has spread to many urban centers and their surroundings, including Manaus and Belém (Pinto 1944, Sick 1968, Oren and Smith 1981). Most of this spread can be linked directly to human actions through the bird trade and intentional liberations of these waxbills (Sick 1968, Oren and Smith 1981).

Escaped birds brought to Belém by bird dealers in the 1970s are probably responsible for the local establishment of this species. We have observed the Common Waxbill in the following districts: Cidade Velha, Guamá, Marco, Marambaia, Nazaré, São Braz, Souza, and Telégrafo. The population is estimated to be 300–500 individuals.

These birds fed (N = 120 observations) on four species of grasses: *Panicum maximum* (80% of observations), *P. purpurascens* (10%), *Paspalum conspersum* (8%), and *Echinochloa* sp. (2%). The birds were found in groups of 2–25 (median = 18, N = 80 flocks). Flocks diminished in size during the breeding season (Sept.–Dec.). The use of the native grass *Paspalum conspersum* as a seed source for *E. astrild* is interesting, because Oren and Smith (1981) reported that in Manaus the birds ignored other native grasses of the same genus, notably *P. repens*. Many interspecific interactions were observed between *E. astrild* and native finches.

Nesting records are from Sept. (1 nest), Oct. (2), Nov. (1), and Dec. (1). Of these, three were in acacia (*Cassia siamea*) and two in India almond (*Terminalia catappa*) trees, both of Asian origin and widely planted in Belém. The nest, placed 2–3.5 m up, was constructed principally of stems of *P. maximum*. The three nests accessible for inspection contained 4, 4, and 7 eggs, respectively. Peaks of foraging activity were noted at 07:00–09:00 (45% of observations) and 14:00–16:00 (35%). Cloud cover and precipitation were important factors in changes in this general pattern.

Because *E. astrild* is little valued by local bird dealers, it is not persecuted for the cage bird trade. Its population appears to be growing. The species has recently colonized the city of Castanhal, 80 km east of Belém, where it was first recorded in 1984 (JMCS pers. obs.).

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Double-brooding by Florida Burrowing Owls.—While conducting a study to determine the impact of urban development on Florida Burrowing Owls (*Athene cunicularia floridana*), we discovered five instances of double-brooding (defined here as raising two broods in the same calendar year). Double-brooding has not been previously documented in Burrowing Owls (Bent 1938, Butts 1973), but most information on the breeding biology of this species comes from studies of Western Burrowing Owl (*A. c. hypugaea*) populations that are migratory or breeding in areas where climate probably precludes multiple breeding attempts

(Best 1969, Coloumbe 1971, Martin 1973, Gleason 1978, Collins 1979). Studies of non-migratory populations of *A. c. hypugaea* by Thomsen (1971) and Butts (1973) revealed occasional renesting following the destruction of burrows or the loss of eggs or hatchlings. Wesemann (1986) suggested the subtropical climate and stable prey densities in southern Florida might allow double-brooding by *A. c. floridana,* but he observed no double broods during a two-year study in southwestern Florida. This paper describes double-brooding in the same southwestern Florida Burrowing Owl population studied by Wesemann (1986).

Study area and methods.—Observations were made between 1 January 1987 and 1 July 1988 on a 36.2-km^2 study area in Cape Coral, Lee County, Florida. The study area consisted mainly of single-family homes interspersed with vacant lots. Vacant lots, where most nest burrows were situated, were maintained as disclimax grasslands by regular mowing. Climate in Cape Coral is subtropical, with an annual mean temperature of 23.1°C. Temperatures below 0°C are rare; lowest daily mean temperature for January (the coldest month) is 10.9°C. Precipitation averages 125.7 cm annually, and 75% of rainfall occurs between May–September (climate data from NOAA climatological data summaries for Fort Myers, Florida, 20 km southeast of the study area).

From January through March in both years, we drove all roads in the study area searching for Burrowing Owl nest burrows. This approach is known to locate all but a small percentage of nests (Wesemann 1986). Burrows attended by two adult owls or decorated with shredded paper and grass were considered occupied nest sites. Adult and juvenile Burrowing Owls were captured with noose carpets placed at the burrow entrance and were banded with U.S. Fish and Wildlife Service bands. When banded owls were reencountered, we confirmed identification by reading band numbers with spotting scopes or binoculars or by retrapping. The sex of breeding adults could usually be determined at a distance by plumage (males were lighter than females due to increased sun-bleaching [Thomsen 1971, Butts 1973, Martin 1973]) or behavior (Thomsen 1971). Breeding females could be distinguished in the hand by the presence of a large, conspicuous incubation patch. Clutch initiation dates were estimated at successful nest sites (occupied nest sites that fledged at least one young) by back-dating 70 days from the fledging date (assuming an incubation period of approximately 30 days and a nestling period of 40 days; Collins [1979], Henny and Blus [1981], pers. obs.). Juveniles were considered fledged if, when approached, they flew away rather than retreated into the burrow. Nests were examined weekly, and the midpoint of the interval between the observed fledging date and the last previous visit was used as the actual fledging date.

Results.—We located 149 occupied Burrowing Owl nest sites in 1987 and 160 in 1988. Egg laying occurred from about 10 December to 18 April, in the 1986–1987 breeding season, and from about 2 October to 9 May in 1987–1988 (Fig. 1). The median clutch initiation date was 15 March in both years.

In 1986, at least three Burrowing Owl pairs laid eggs about 10 December, before we initiated surveys. We banded both adults at each of these nests in January 1987, as well as three of four juveniles in February 1987. One juvenile fledged at each of two nests (nests A and B), and two young fledged at the third (nest C). Fledging occurred on about 25 February 1987. Adults at nests A and C remained paired, and by mid- to late March 1987 exhibited signs of renesting (e.g., burrow decoration). The pair at B separated on about 22 February 1987, when the banded male from nest B paired with a different banded female at a new burrow (nest D) 30 m away. His previous mate and the fledged juvenile remained at nest B.

On 22 May 1987, nonflying young were observed again at nests A and C. In both cases, these juveniles were attended by the same adults that attended the earlier broods. Five young fledged at nest C about 21 May 1987, and three fledged at nest A about 3 June 1987. We estimated that second clutches were initiated at nests C and A on 13 March 1987 and 26 March 1987, respectively. Juveniles from the first brood were not observed at nest A after

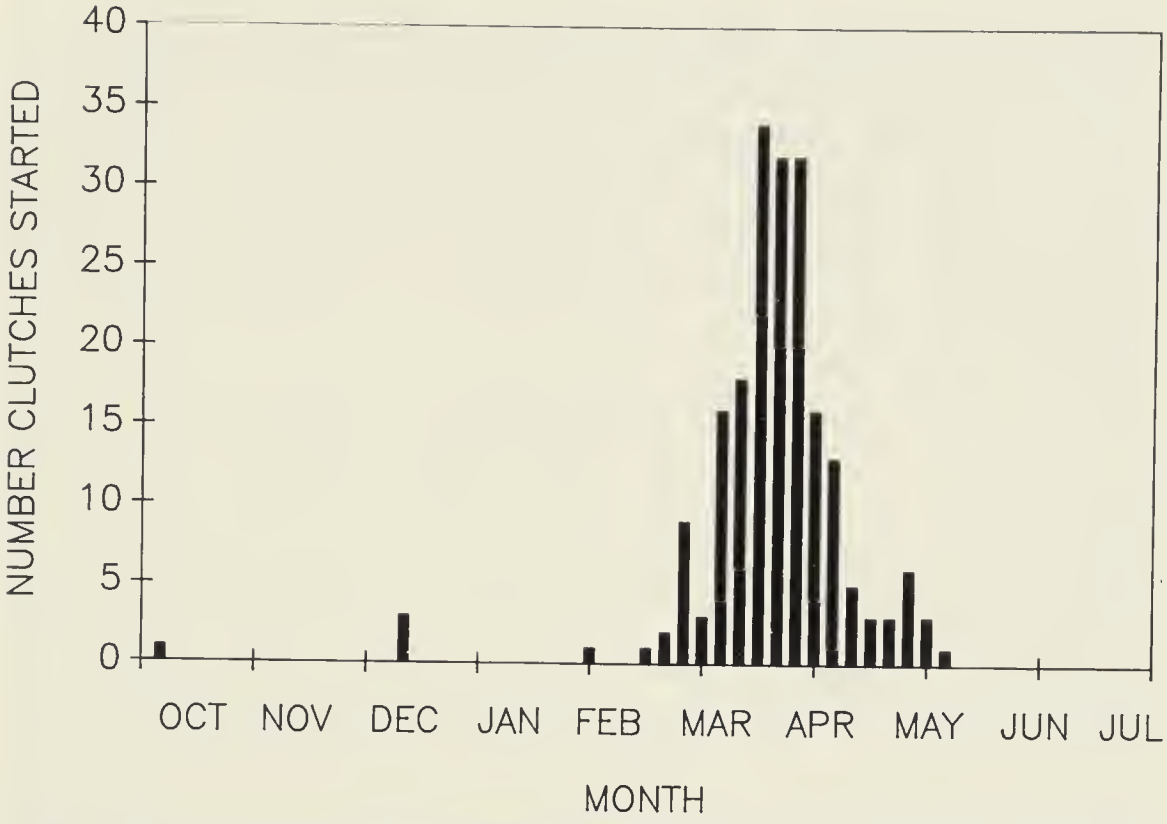

FIG. 1. Nesting chronology of Florida Burrowing Owls in Cape Coral, Florida, December 1986–July 1988. Data for both years are pooled since the median laying date (15 March) was the same.

mid-March 1987. The single juvenile from the first brood at nest C moved to a new burrow 50 m away in mid-March; we observed no subsequent interactions between this owl and the adults at nest C.

We observed nonflying young at nests B and D on 23 May 1987. The brood at nest D was attended by the male that had earlier nested at B and his new mate. Nest B was attended by the adult female present earlier and her son from the first brood (the sex of this juvenile was confirmed in the 1987–1988 breeding season). The juvenile actively defended nest B from human intruders, but he was not observed bringing food to his mother or to the second brood. The male at nest D actively defended that nest and captured food for that brood, but he showed no attachment to nest B or to his previous mate after 22 February 1987. Four juveniles fledged at nest B and three fledged at nest D on about 31 May 1987. We estimate that clutches at both nests were initiated about 23 March 1987.

A fourth pair of Burrowing Owls (nest E) fledged three young on about 2 May 1987 (egg laying occurred about 23 February 1987). The same male and a different unbanded female initiated a clutch at nest E about 2 October 1987. Two young fledged at this nest about 12 December 1987. There were no subsequent breeding attempts at this nest in the 1987–1988 breeding season.

The approximate interval between fledging of first broods and initiation of second clutches was 29 days at nests A and D, 26 days at nest B, and 16 days at nest C. The interval at nest E was approximately 150 days.

Discussion.—Our observations confirm Wesemann's (1986) prediction that double-brooding could occur in Florida Burrowing Owls, although it appears to be a rare event (1% of

occupied nests in our study population over two years). Additional observations will be required to identify circumstances that lead to double-brooding in this population.

The paternity of the second brood at nest B is uncertain. The original pair at this nest separated 29 days before the second clutch at B was initiated. The only male Burrowing Owl observed at nest B during this 29-day interval was the son from the earlier brood. Thus, there are four possibilities regarding paternity: (1) the original male at nest B mated polygynously with females at both nests B and D; (2) the second clutch at nest B was fertilized by sperm stored from copulations prior to 22 February 1987; (3) the clutch was fertilized by the male offspring of the first brood; or (4) fertilization resulted from extra-pair copulation(s) with an unknown male.

While we cannot rule out possibilities (1) and (4), they are not consistent with our observations (i.e, on our weekly visits between 22 February and 23 March 1987 we observed no interactions between the original pair and saw no foreign males in the vicinity of nest B). Possibility (2) is contingent on sperm storage capabilities in female Burrowing Owls. Although sperm storage glands have not been described in this species, they are present in many avian orders (Hatch 1983). In species that have been studied, sperm remains viable in the storage glands for 6 to 60 days, although fertilization capability appears to decrease with time (Hatch 1983).

Even if fertilization resulted from stored sperm, it is unlikely that the female at nest B could produce a full clutch of eggs without a mate to supply her with food. Our observations indicate that females at successful nests gain so much weight prior to egg laying that some are unable to fly for several days prior to clutch deposition. During this time and throughout the laying period, females seldom leave the nest burrow and are probably totally dependent upon the male for food and nest defense. Newton (1986) reports a similar dependence on males by female Eurasian Sparrowhawks (*Accipiter nisus*) during egg laying. Unassisted female Burrowing Owls would be hard-pressed to reach the physiological condition necessary for egg laying or to lay a clutch of normal size. For this reason, we believe that the son from the first brood at nest B probably provisioned his mother during laying and incubation, whether or not he was the father of the second brood. The adult female at nest B died in July 1987, and her son subsequently paired with an unbanded female. Thus, we were unable to confirm whether the mother and son were a mated pair.

Parent-offspring matings are not uncommon in our study population. During the 1987–1988 breeding season, four such pairs were found; three males paired with their mothers and one female paired with her father. This represents 13% of all pairs where both adults were identified (N = 31). The age at which Burrowing Owls become sexually mature is unknown, but we have observed copulation attempts between 80-day-old siblings, and one-year-old males and females (including one of the mother-son pairs noted above) nested successfully on our study area in the 1987–1988 breeding season.

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Was the Socorro Mockingbird (*Mimodes graysoni*) a predator on small birds?—The endemic avifauna of Isla Socorro, of the Revillagigedo archipelago, Mexico (lying ca 400 km SW of the tip of Baja California), includes four passerines: the Socorro Wren (*Thryomanes sissonii*), which looks as much like a House Wren as a Bewick's Wren; a distinctive form of the Tropical Parula (*Parula pitiayumi graysoni*) that was considered a full species as recently as the 5th edition of the AOU Check-list (AOU 1957); a small (30 g) race of the Rufous-sided Towhee (*Pipilo erythrophthalmus socorroensis*), also given species status in that check-list; and the Socorro Mockingbird (*Mimodes graysoni*), considered an endemic monotypic genus. Formerly called "Socorro Thrasher," this bird appears in the field to be more similar to mockingbirds. However, in a cladistic study of the Mimidae, Gulledge (1975) was unable to resolve a trichotomy that included *Mimus* (the typical mockingbirds), *Mimodes*, and *Toxostoma* (the thrashers).

Once considered "the most abundant and widely distributed species" on Isla Socorro (McLellan 1926), *Mimodes graysoni* was almost completely extirpated by 1981, probably by feral cats descended from pets brought to the island after the establishment of a military base in the late 1950s (Jehl and Parkes 1982, 1983).

Almost nothing is known of the life history of *Mimodes*, particularly its feeding behavior, in a natural state. The only published statement on foraging I have found is that of Brattstrom

and Howell (1956), who described a group of Socorro Mockingbirds feeding on blowflies congregated on the carcasses of sheep.

The California Academy of Sciences houses the unpublished field notes of Sterling Bunnell, a member of the Academy's 1903 expedition to Isla Socorro (Baptista 1987). Like several other observers, Bunnell commented on the tameness of the Socorro Mockingbirds. He stated that they were especially fond of cheese, and raided the food (unspecified) provided for the expedition's live parrots (presumably the endemic race of Green Parakeet, *Aratinga holochlora brevipes*). In commenting on their tameness, Villa (1960) described mockingbirds entering his tent to feed on bread. Some of the few remaining individuals of this species that we found on our 1978 expedition had maintained their traditional tameness, possibly because of a nearby picnic site of the military personnel, where the birds may occasionally have been fed.

None of this, however, throws any light on the *natural* foods of *Mimodes,* other than to suggest that, like other mimids, it was omnivorous. The only confirmation of this suggestion is from Bunnell, who wrote: "They eat many rose berries and the black berry on trees high on the mountain . . . Eat dead crabs."

Prior to human settlement of Socorro, its fauna included no mammals, one small lizard (*Urosaurus auriculatus*), an Elf Owl (*Micrathene whitneyi graysoni*) that Grayson (1872) described as feeding on insects and small crabs, and a Red-tailed Hawk (*Buteo jamaicensis socorroensis*) known to feed on crabs, doves, and probably lizards. The endemic race of Yellow-crowned Night-Heron (*Nycticorax violaceus gravirostris*), like members of its species elsewhere, feeds largely on crabs. None of these is likely to have been a principal predator on the small passerines, not even the Red-tailed Hawk, which would be unlikely to negotiate the tangled vegetation inhabited by the three species of songbirds.

One normally expects that in any ecosystem, most species will have one or more identifiable principal predators. I suggest that *Mimodes* was the principal predator on the three smaller species of passerines, most likely on their eggs and nestlings. At least one other large insular mimid, the Pearly-eyed Thrasher (*Margarops fuscatus*) of the West Indies, is a major nest predator (see, for example, Wiley and Wiley 1979). That this role was filled on Isla Socorro by *Mimodes* is supported by two lines of circumstantial evidence. The first involves mobbing. In 1981, when I was walking through an area occupied by mockingbirds in 1978 and playing back the songs recorded that year, I was mobbed by towhees, wrens, and warblers. Mainland towhees respond dramatically to my "squeak," but those on Isla Socorro have lost their traditional tameness, and were hard to lure into sight. However, the towhees approached me much more closely in response to playbacks of the Socorro Mockingbird tapes than they ever had in response to "squeaking." The behavior of the wrens and warblers as well as the towhees was similar to that shown by many species of small birds in mainland Mexico in response to my imitation of the whistle of the Ferruginous Pygmy-Owl (*Glaucidium brasilianum*). The birds mobbed me *only* during the playback, and were not simply responding to my presence. I can see no explanation for this behavior other than a reaction to a perceived threat, in this instance the voice of a known nest predator.

Indirect evidence for the Socorro Mockingbird's status as predator on the small passerines involves recent changes in the relative abundance of species. Those most affected by the cat predation appear to have been the mockingbird and towhee, the Socorro Dove (*Zenaida graysoni*), now considered extinct in a wild state, and Townsend's Shearwater (*Puffinus auricularis*) (Jehl and Parkes 1982, 1983), all ground-nesting or ground-foraging species. The tree-nesting warbler and wren appear not to have been affected by cat predation. We found both to be as tame as ever, and judging from descriptions in the literature, probably even more abundant than they were at the time of previous visits by ornithologists. Brattstrom and Howell (1956), reporting on Brattstrom's visit in 1953, said that the wren was "fairly common in most habitats, but was most numerous in the non-forested portions below

2000 feet." Jehl and I reported in our 1982 paper that the wren was "second in abundance to the Tropical Parula, [and] occurred at every locality we visited. . .up to the crest of Cerro Evermann (1040 m)." Even more striking is the apparent increase in the warbler population. Brattstrom and Howell wrote that these birds were "fairly common at lower elevations . . . but they seemed scarcer than the other endemic land birds although equally tame and easy to approach." In contrast, our paper states that, at Grayson's Cove in particular, the wren was outnumbered about 10:1 by the parula, which we considered to be by far the commonest land bird on the island, a status that was assigned to the mockingbird in the report of the California Academy of Science expedition of 1925 (McLellan 1926). In what appeared to be areas of food abundance, we saw gatherings of as many as 30–50 warblers. They occurred in habitats from the beachside vegetation to within 50 m of the crest of Cerro Evermann. This abundance is in stark contrast to the current status of those species most vulnerable to cat predation.

Based on our field experience in 1981, Jehl and I found it difficult to believe that the Socorro Mockingbird could have persisted, and certainly not in significant numbers. On 10 November 1984, five observers visited Isla Socorro briefly by air, spending about 5.5 h birding on foot. Although Jehl had supplied the party with our 1978 tapes of *Mimodes* vocalizations, only the recent immigrant Common Mockingbird (*Mimus polyglottos*) responded. Another survey, made by a party from the University of Mexico in August 1987, found about 20 individuals of *Mimodes* in a relatively inaccessible part of the island. The avian ecosystem of Isla Socorro is obviously in a dynamic stage at present. The Socorro Mockingbird is now outnumbered by the self-introduced Common Mockingbird (Jehl and Parkes 1983; S. Howell pers. comm.), a species unlikely to have a predatory impact on the smaller passerines. On the other hand, American Kestrels (*Falco sparverius*) have reached Isla Socorro (J. F. Clements and S. Howell pers. comm.) In 1984 the wren and warbler populations were reported still to be high. It remains to be seen whether the small remaining population of *Mimodes* is viable, and whether the carnivorous/insectivorous kestrel will become a major predator on the warbler and wren (probably on adults rather than on eggs and nestlings) and eventually establish a new predator-prey equilibrium on Isla Socorro.

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Winter diets of vultures in Pennsylvania and Maryland.—Black Vulture (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) have declined in recent decades (Brown 1976). Food habits of these two species have been examined by analysis of regurgitated-pellets or by behavioral observations of marked birds at single roosts (Paterson 1984, Yahner et al. 1986, Coleman and Fraser 1987). No studies have compared winter food habits of vultures among communal roosts. Our objectives were to: (1) compare winter diets of vultures at seven communal roosts in southern Pennsylvania and northern Maryland, and (2) determine if food remains constituting winter diets were related to potential availability of these remains or to habitat features in the vicinity of roosts.

Study area and methods.—We conducted the study at seven winter communal roosts used by Black and Turkey vultures; each roost was located in a different county of southern Pennsylvania and northern Maryland (Thompson 1987). Major land uses in these counties were forest, agriculture, and residential (U.S. Bureau of the Census 1986). One-hundred ninety-two pellets were gathered at the seven roosts (N = 21–30/roost) in early to mid-February 1987. All visible pellets were gathered during a single visit to a roost to minimize differences in the effects of weather (e.g., depth of snow cover) on food items used by vultures (see Yahner et al. 1986). Based on appearance, we estimated that pellets collected were less than two weeks since egestion. Distances between roosts varied from 31 to 163 km and averaged 106 ± 41 km [SD]. Mean numbers of wintering Black and Turkey vultures/roost were 65 ± 65 [SD] and 136 ± 122, respectively (Thompson 1987). We have no evidence that vultures were segregated by species within roosts (Yahner et al. 1986, Thompson 1987).

TABLE 1

PERCENT OCCURRENCE OF ANIMAL FOOD REMAINS AND NUMBER OF ROOSTS IN WHICH A PARTICULAR FOOD REMAIN WAS CONTAINED IN PELLETS

Food remains	Percent occurrence	Number of roosts
Domestic poultry		
Chicken (*Gallus gallus*) and Turkey (*Melagris gallapavo*) combined	64.1	7
Large domestic mammal		
Cow (*Bos taurus*)	32.3	7
Pig (*Sus scrofa*)	8.9	6
Sheep (*Ovis aries*)	6.8	5
Goat (*Capra hircus*)	2.6	2
Subtotal	50.5	7
White-tailed deer (*Odocoileus virginianus*)	40.1	7
Small mammal		
Virginia opossum (*Didelphis virginiana*)	6.8	5
Eastern cottontail (*Sylvilagus floridanus*)	11.5	4
Gray squirrel (*Sciurus carolinensis*)	2.1	3
White-footed mouse (*Peromyscus leucopus*)	0.5	1
Meadow vole (*Microtus pennsylvanicus*)	3.6	2
S. red-backed vole (*Clethrionomys gapperi*)	0.5	1
Striped skunk (*Mephitis mephitis*)	4.7	4
Raccoon (*Procyon lotor*)	2.6	2
Domestic cat (*Felis catus*)	7.3	5
Subtotal	39.6	6
Miscellaneous bird		
Unidentified vulture	7.3	5
Unidentified passerine	1.0	2
Subtotal	8.3	5
Plant material	81.8	7

Pellets egested by Black Vultures could not be distinguished from those egested by Turkey Vultures, so data were pooled from both species (Yahner et al. 1986, Coleman and Fraser 1987).

We oven-dried pellets for 24 h and separated them under a dissecting microscope. Cuticular scale patterns of hairs and intact hairs were examined with a stereoscope or a compound microscope and compared to reference slides and a hair guide (Adorjan and Kolenosky 1969) to identify animal species (Yahner et al. 1986). All white feathers were presumed to be domestic chicken (scientific names in Table 1) or domestic turkey, because both species were abundant in counties containing the roosts (U.S. Department of Commerce 1984a, b). Presence or absence, rather than volume, was noted for each animal food remains because of differences in digestibility of animal food (Coleman and Fraser 1987). Occurrence of plant material, but not the species, also was noted for each pellet.

We determined the frequency of occurrence of each animal food remain based on the total number of pellets in which a given animal species occurred in pellets from each roost. Animal food remains were placed in five general categories: domestic poultry, large domestic mammal, white-tailed deer, small mammal, and wild bird. Frequencies of occurrence of remains in each category, based on presence or absence of remains in the total number of pellets/roost, were compared among roosts using 2×7 G-tests-of-independence (Sokal and Rohlf 1981:744); if frequency of a category was significant ($P < 0.05$) among roosts, a 2×2 G-test-of-independence was used about the roost of interest to determine whether or not frequency of occurrence differed significantly ($P < 0.05$) from expected (Sokal and Rohlf 1981:744).

Percent similarity in winter pellets was determined for each pair of roosts using the proportional similarity index (Brower and Zar 1984:161). Food remains used to calculate the index were individual species of animals that occurred in at least 15 of the 192 pellets and included poultry, domestic cow, domestic pig, deer, and eastern cottontail. Relationships between percent similarity and distance (km) separating each pair of roosts were determined by product-moment correlation analyses of untransformed and log-transformed data (Sokal and Rohlf 1981:565).

County-wide production of livestock and poultry (U.S. Department of Commerce 1984a, b) and county-wide numbers of harvested and road-killed deer combined (Pennsylvania Game Commission and Maryland Department of Natural Resources, unpubl.) were used to represent the potential availability of animal food to vultures (Thompson 1987). These data were compared to frequencies of occurrence of poultry, large domestic mammals, and deer in pellets from a roost in a corresponding county via product-moment correlation analyses. We also examined associations between frequencies of occurrence of the five categories of animal food remains with 10 habitat features of roosts, using correlation analyses. These features, described by Thompson (1987), were percent slope at roost center; cover-type diversity (CD) within a 1.6-km radius of a roost, where $CD = \Sigma p_i \log_e p_i$, with p_i = proportion of the ith cover type within a 1.6-km radius of a roost; interspersion of cover types (Heinen and Cross 1983), both within a 1.6-km radius of a roost and immediately adjacent to a roost; distances (m) of a roost to the nearest road, occupied human habitation, food resource (e.g., cattle feedlot, poultry farm), and lake; and land-surface ruggedness (Beasom et al. 1983) within a 40-ha circle superimposed over the center of a roost and within a 1.6-km radius of a roost.

Results and discussion.—Animal food remains from 16 species were found in our sample of 192 pellets (Table 1). Poultry and large domestic mammal remains occurred most frequently in vulture pellets from the seven roosts. Deer and small mammal remains occurred less often in pellets. Eastern cottontails, domestic cats, and Virginia opossums were the predominant small mammal remains in pellets. Vulture feathers in pellets were probably ingested while preening. Plant material was found in 82% (N = 157) of the pellets.

Our study, and others in the Mid-Atlantic states (e.g., Paterson 1984, Yahner et al. 1986, Coleman and Fraser 1987), have shown that wintering vultures occupying communal roosts depend on a variety of domestic and wild carrion. In these studies, remains of poultry, large domestic mammals, and deer occurred in a high proportion of vulture pellets. Use of carrion of domestic cattle by vultures might be greater than that actually obtained from regurgitated-pellet analysis, because offal and afterbirth from cattle do not show up in pellets (Coleman and Fraser 1987). As in our study, plant material can occur in a large proportion of pellets (Paterson 1984, Prior 1986). We are uncertain whether plant material was ingested purposely or perhaps accidently by vultures feeding on carrion (Paterson 1984).

Occurrence of poultry, large domestic mammals, and small mammals in vulture pellets differed among roosts (Table 2). In general, occurrence of domestic animal food remains

TABLE 2

PERCENT OCCURRENCE OF FOUR CATEGORIES OF ANIMAL FOOD REMAINS IN VULTURE PELLETS COLLECTED DURING FEBRUARY 1987

Category	Roost, county, and state						
	Big Round Top Adams, PA (N = 30)	Meadow Grove Perry, PA (N = 21)	Mount Gretna Lebanon, PA (N = 30)	Muddy Run York, PA (N = 30)	Octararo Lake Chester, PA (N = 21)	Deep Run West Carroll, MD (N = 30)	Lake Linganore Frederick, MD (N = 30)
Domestic:	83.3	95.2	100.0	83.3	95.2	80.0	73.3
Poultry[a]	60.0	52.3	100.0[b]	56.7	85.7[b]	43.3[c]	53.3
Large domestic mammal[a]	36.7	100.0[b]	40.0	33.3[c]	57.1	50.0	50.0
Wild:	80.0	23.8	50.0	23.3	57.1	66.7	70.0
White-tailed deer	56.7	28.6	33.3	26.7	33.3	40.0	56.7
Small mammal[a]	63.3[b]	0.0[c]	36.7	10.0[c]	47.6	73.3[b]	46.7

[a] Species comprising each category are given in Table 1. Observed frequency of occurrence was significantly different from expected; $P < 0.01$, 2×7 G-test-of-independence.
[b] Frequencies of a food item were significantly ($P < 0.05$) greater than expected.
[c] Frequencies were less than expected based on 2×2 G-tests-of-independence about the roost of interest.

(poultry and large domestic mammal) in pellets/roost varied from 73.3% (Lake Linganore Roost) to 100.0% (Mount Gretna Roost); occurrence of wild remains (deer, small mammal, wild bird) varied from 23.3% (Muddy Run Roost) to 80.0% (Big Round Top Roost). Vultures used poultry extensively at Mount Gretna and Octararo Lake, large domestic mammals at Meadow Grove, and small mammals at Big Round Top and Deep Run West. Use of deer did not differ from expected ($0.05 < P < 0.10$) at any roost but was highest (>56%) at Big Round Top and Lake Linganore.

Paterson (1984) noted a 70% use of poultry by vultures in a Virginia roost. At the Big Round Top Roost, poultry occurred in 60.0% of the pellets in 1987 (present study) but in only 49.0% of the pellets in winters 1982–83 and 1983–84 (Yahner et al. 1986). Similarly, frequencies of occurrence of large domestic mammals in vulture pellets differed among roosts, ranging from 16.4% (Coleman and Fraser 1987) to 100% (Meadow Grove Roost, present study).

Although Turkey Vultures use smaller carrion (e.g., small mammals) more often than Black Vultures (based on observations of marked birds; Coleman and Fraser 1987), use of small mammals by vultures can vary widely among roosts (e.g., 0%, Meadow Grove; 73.3%, Deep Run West). However, there is no direct evidence that use of smaller carrion by the less aggressive Turkey Vulture is a result of use of larger carrion (e.g., deer) by the more aggressive Black Vulture (Coleman and Fraser 1987).

Percent similarity in use of animal food remains between roosts ranged from 58 to 91% ($\bar{x} = 75 \pm 8\%$). Greatest similarity was found between Muddy Run and Mount Gretna Roosts (91%), which were 84 km apart, and between Big Round Top and Deep Run West roosts (90%), which were 35 km apart. Least similarity occurred between Meadow Grove and Big Round Top roosts (58%) which were 100 km apart. Percent similarity and distance (km) between roosts were not correlated ($r = -0.34$, df = 19, $P > 0.05$).

Frequencies of occurrence of poultry, large domestic mammals, cows, or deer were not associated with county-wide production of domestic animals or with county-wide deer

harvests or roadkills combined (r's = −0.73 to 0.24, df = 5, $P > 0.05$). Three reasons might account for our inability to find a relationship between occurrence of remains and county-wide indices of potential food. First, vultures are opportunistic foragers and rely on localized, emphemeral food resources (Sweeney and Fraser 1986). Second, the availability of carrion of domestic animals varies among landowners, depending on how they comply with local animal disposal laws (Coleman and Fraser 1987). Third, our pellet samples were taken during one month in winter. If we had the opportunity to examine more pellets/roost or pellets among seasons, perhaps relationships between diet and potential food availability would become more evident.

Frequencies of occurrence of deer in pellets/roost and numbers of deer harvested and road-killed in a given county also were not associated, because use of deer by wintering vultures might be a localized rather than a county-wide phenomenon. For instance, in our study and in others (Yahner et al. 1986, Coleman and Fraser 1987), deer were an important food source for vultures in the immediate vicinity of the Big Round Top Roost. Numbers of road-killed deer near Big Round Top Roost are much higher than elsewhere in Adams County (H. Greenlee and L. Haines pers. comm.).

Availability of small mammals during winter may decline because increased snow cover presumably reduces the ability of vultures to find road-killed small mammals (Yahner et al. 1986). Yahner et al. (1986) found that small mammals occurred in 20.9% and 9.3% of vulture pellets during snow-free (snow depth <7.6 cm) and snow-covered periods (>7.6 cm), respectively. In the present study, snow cover seldom exceeded 7.6 cm in February, thereby possibly accounting for high use of small mammals in most roosts in winter 1987.

Frequencies of occurrence of poultry in vulture pellets were correlated with land-surface ruggedness within 40 ha of a roost ($r = -0.79$, df = 5, $P < 0.05$), both large domestic mammals and cows with slope ($r = 0.86$, df = 5, $P < 0.05$) and land-surface ruggedness within a 1-km radius of a roost ($r > 0.79$, df = 5, $P < 0.05$), and deer with interspersion of cover types immediately adjacent to a roost ($r = -0.87$, df = 5, $P < 0.05$). Frequencies of occurrence of small mammals in pellets were not related ($P > 0.05$) to habitat features of roosts.

Relationships between diet and habitat features in the vicinity of roosts were difficult to interpret. For example, in Pennsylvania, a mix of farm and forest habitats are associated with high deer densities (Storm and Yahner, unpubl. data), and hence frequencies of deer in pellets might be expected to increase with interspersion of farm and forest types immediately adjacent to a roost. However, we found an indirect relationship between deer in pellets and cover types in our study. Although habitat features associated with roosts measured in our study may not be helpful in predicting winter diets of vultures using a given roost, they have been found to be important in roost-site selection by vultures. Wright et al. (1986) and Thompson (1987), for instance, found that mature coniferous stands were selected as communal roosts by wintering vultures in southern Pennsylvania and northern Maryland.

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Singing behavior of American Robins in linear and non-linear habitats.—This study documents a difference in singing behavior between two populations of American Robins (*Turdus migratorius*) inhabitating neighboring but dissimilar areas. To our knowledge, significant interpopulation differences in response to playback have not been reported previously.

In the northern plains of the United States, trees and shrubs growing along creeks and rivers or in shelterbelts provide the only natural nesting sites for tree-nesting birds such as

robins (Yahner 1982, Haas, pers. obs.). Shelterbelts typically are planted as long, narrow rows of trees. We term this "linear" habitat because the average width is considerably less than the average diameter of territories of robins studied in other localities (Young 1951, Pitts 1984).

We observed that robins in shelterbelts sang less frequently than those in riparian woodlands. We hypothesized that the reduced singing by shelterbelt-inhabiting robins indicated less defense of the linear habitat which they occupy, compared with woodland-inhabiting riparian robins. Average territory size for robins in New York, Tennessee, and Wisconsin ranged from 0.11 to 0.21 ha (Pitts 1984). Territories of the same size in shelterbelts would need to be much longer than wide, a theoretically uneconomical shape for a bird's territory (Covich 1976), although Johnston (1956) observed Song Sparrows (*Melospiza melodia*) defending 30 × 150-foot territories along tidal sloughs. Reduced territoriality should result in a lower response to playback, and we predicted that robins breeding in linear habitat would show this reduced response.

Methods.—We collected data from May through July 1987 and June and July 1988, in Sioux and Morton counties, North Dakota. The shelterbelts were located in mixed-grass prairie, range, and farmyards on an 8 × 11-km area of private land. The riparian habitat studied was part of Fort Abraham Lincoln State Park, 8 km south of Mandan, North Dakota, and 35 km from the shelterbelts.

Local shelterbelts—trees and shrubs planted in one to eight rows as windbreaks around farm buildings and fields—consisted primarily of green ash (*Fraxinus pennsylvanicus*), American and Siberian elm (*Ulmus americana* and *U. pumila*), box-elder (*Acer negundo*), Siberian pea-shrub (*Caragana arborescens*), and Russian olive (*Eleagnus angustifolia*). Trees in these shelterbelts were 3.3–15 m tall, and most of the shrub layer had been destroyed by livestock. The average width of this habitat type was 10 m. The woodland or non-linear habitat type occurred along the Missouri River. This floodplain forest consisted of mature cottonwoods (*Populus deltoides*), box-elder, American elm, and green ash, and it had an abundant shrub layer, including *Cornus* sp., *Rosa* sp., and *Lonicera* sp. Most of the canopy trees reached heights of approximately 20 m. Width of this area was 400–1000 m.

Adult robins were mist-netted, color banded, tail-painted, and released. We observed a total of 26 males at the riparian site and 23 in shelterbelts, almost all associated with known nests. All robins used in playback experiments had active or recently fledged nests. We confirmed identification of the male robin associated with a nest by repeated observations. Nesting phenology did not differ significantly between the two habitats. Using 1 May as day 1, the mean hatching date of 18 riparian nests was 41.42 and of 26 shelterbelt nests was 42.67 ($Z = 0.28$, $P > 0.3$). For robins in shelterbelts, we determined number of neighbors by referring to daily maps of sightings and nests of marked individuals. We defined a neighbor as a male with a territory contiguous with that of the male of interest.

For both focal observations and playback experiments, we recorded time of day, nest stage, initial behavior of bird, color-band combination of bird, location, and date. Focal observations never followed playback trials.

Songs from birds in each habitat type were recorded using a Marantz 221 recorder and a 15″ parabola. These birds were not tested in later playback trials. Tapes of two robins from New York (Newfield and Library of Natural Sounds) also were used in playback experiments. During the experiments each of these four recordings elicited song in response to playback from at least two individuals. Use of different songs reduces the possibility of obtaining biased responses as a result of playing tapes from atypical males (Kroodsma 1986). We used each tape with the following frequencies in riparian and shelterbelt habitat respectively: Newfield 3,3; Library of Natural Sounds 4,3; Fort Lincoln 3,3; shelterbelt 1,7. Only one song was played during each playback trial. Individual males were used in one or

two trials. Individual birds were not tested more than once in a two-day period so as to reduce acclimatization to song. At each site, approximately one-third of the playback experiments were conducted during each of three time periods: morning (0600–1000 CDT), mid-day (1001–1400 CDT), and late afternoon (1401–1800 CDT). For playback, we placed a Realistic C.B. Extension speaker connected to a Realistic Minisette IV cassette player from ground level to 2.4 m high on fences or trees. The speaker was located within 30 m of the nest of the experimental male. In one of the four trials using birds with recently fledged nests, the speaker was located 52 m from the fledged nest. For each trial, the song used was that of a non-neighboring individual. We located the target male prior to beginning the tape and recorded changes in his behavior after playback began. We noted times of beginning and ending response, latency to first response, closeness of approach, and singing behavior. These measures are considered accurate indicators of aggression levels (at least one aspect of territoriality) (Catchpole 1977). To determine singing rates, we initiated observations immediately after a marked male was located. Most observations were of birds located by sight in both habitat types. Males were followed for as long as possible (up to 15 minutes), and the number of minutes in which each sang was recorded.

Results and discussion.—Robins in the riparian habitat sang in response to playback in significantly more instances (9 of 11 trials) than did robins in the linear habitat (5 of 20 trials) (Fisher's exact test, $P = 0.01$). These results indicate that robins in the non-linear riparian habitat are more likely to respond with song to intruders than are robins in linear shelterbelts. Robins in both habitat types were equally likely to orient or move towards the speaker (10/11 in riparian habitat, 10/17 in shelterbelts; $\chi^2 = 3.36$, 1 df, $P > 0.10$), and exhibited similar closeness of approach to the speaker (10 m in riparian habitat, 9 m in shelterbelts; $t = 0.45$, 15 df, $P > 0.5$).

There were no significant differences between robins in the two habitats in latency to response or length of response to playback. Ten males at each site responded to playback. Including only these birds, mean latency to response in riparian habitat was 51.2 seconds and 58.8 seconds in shelterbelts ($t = 0.40$, 18 df, $P > 0.5$). The mean length of response was 140.7 seconds in riparian habitat and 81.7 seconds in shelterbelts ($t = 1.58$, df = 18, $P > 0.1$).

When we compared the results of focal observations of only those birds known to have active nests, robins in the riparian habitat sang significantly more frequently (in 34 of 195 minutes) than did robins in shelterbelts (in 38 of 353 minutes) ($\chi^2 = 4.9$, 1 df, $P < 0.05$). When we included all birds in the comparison, the significance of the difference increased. Riparian robins sang significantly more frequently (in 92 of 337 minutes) than did robins in shelterbelts (in 58 of 444 minutes) ($\chi^2 = 25.1$, 1 df, $P < 0.001$). There are two possible explanations for the less significant differences observed when using only data from robins known to have nests. The change may be due simply to the change in sample size or due to a propensity of robins without nests to sing more often. Unmated male passerines may sing more frequently than mated males (Catchpole 1977). The status of males for which we could not find nests in the riparian habitat is uncertain. These males may have had active nests that we were unable to locate, but more probably they were not nesting at that time. We believe that unmated males are rare in shelterbelts, because territories where a bird is known to have died are rarely reoccupied, and because we find nests for almost all males in shelterbelts.

The more open structure of shelterbelts may make visual contact between birds easier, thereby decreasing aggressive interactions and the need for song to maintain territories or attract mates. Alternately, riparian robins may defend their territories or mates more actively than do shelterbelt robins because their territories are of higher quality or because intrusion presents a greater risk. In shelterbelts, robins with no neighbors sang significantly less in

response to playback (0 of 8 trials) than did robins with one or more neighbors (5 of 7 trials) (Fisher's exact test, $P = 0.014$). Because of the geometry of the habitat, riparian birds could be surrounded by neighbors, and encounters between males should be more frequent. Males in shelterbelts, however, rarely can have more than two neighbors. The lower singing rates and response to playback indicate that robins breeding in shelterbelts exhibit reduced territorial defense, probably due to the small number of neighboring males.

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Early experience and vegetation preferences in Common Tern chicks.—The importance of physiognomic features in habitat selection has been studied in both the field and laboratory (Klopfer 1963, Gluck 1984). Noseworthy and Lien (1976) studied the ontogeny of nesting habitat preference in neonatal Herring Gull (*Larus argentatus*) chicks in nature. Herring Gull chicks preferred the nest site during the first week; thereafter this preference waned but never disappeared. However, Noseworthy and Lien's (1976) tests were conducted in the field where colony sounds and the presence of parents could affect the outcome. Although field studies are very useful in developing habitat recognition paradigms, laboratory studies under controlled conditions are necessary to isolate the effect of particular factors. Wiens

(1970, 1972) examined the role of experience on anuran habitat selection, and he reported that tadpoles raised over featureless or striped substrates showed no preference while those raised on a background of squares preferred their natal substrate. Similarly, Eurasian Linnets (*Acanthis cannabina*) raised with natural foliage preferred the species that they were reared on, while those reared with plastic perches showed no preferences (Gluck 1984). In the laboratory, gull chicks *Larus* also showed a preference for natal conditions (Evans 1970). These experiments consistently show preferences for the habitat which young organisms experience, a situation known as habitat imprinting. However, animals were not given a choice of natural habitat features that might be equally attractive. In nature, animals are not only exposed to substrate and vegetation variations in their environment, but many young vertebrates are also exposed to siblings. Siblings may serve as clues to appropriate habitats or locations.

Habitat selection in adult birds could reflect the operation of innate mechanisms, or of learned mechanisms (imprinting), or of both (Lack and Venables 1933, Miller 1942). Early studies focused on behavioral aspects of habitat selection (Klopfer 1965) and the role of habitat selection on reproductive success (Southwood 1977). Recently, there have been numerous studies of habitat selection by nesting birds (see papers in Cody 1985), but there remain few experimental studies of the effect of early experience on either habitat preferences or the shelter sites used to avoid predators or heat stress.

In this paper we examine the role of early experience with vegetation on the behavior of Common Terns (*Sterna hirundo*). Previous studies have not exposed animals under controlled conditions to different, but naturally occurring habitats, to test for the effects of experience on recognition of specific habitat features.

Common Terns nest in a variety of habitats, including *Spartina* salt marshes and vegetated sandy beaches (Austin 1929, Burger and Lesser 1978). On beaches, the terns nest on the ground, often placing their nests close to beach grass (*Ammophila breviligulata*), seaside goldenrod (*Solidago sempervirens*), or other vegetation or debris. Vegetation provides shade from sun, shelter from heavy rains or wind, and protection from predators. Common Tern chicks are semi-precocial at hatching and within hours walk about near the nest. After hatching, siblings usually remain together and stay in or near the nest for two or three days. They begin to move about the territory thereafter but remain close to the nest unless disturbed. By a week to 10 days, chicks typically wander about the territory, are often left alone by parents, and frequently hide under vegetation to avoid thermal stress, heavy rains, or predators. We predicted that young chicks would quickly learn familiar landmarks in their territories. We designed a series of experimens to test this prediction.

Methods.—One chick was collected on the day of hatching from each of 24 nests on 30 June 1984 and from each of 28 nests on 14 July 1986 from Barnegat Bay, New Jersey, and brought into the laboratory. The chicks were weighed, color banded for individual identification, and placed in the rearing cages in groups of four chicks (functional sibgroups). Thus the siblings we speak of shared the same rearing cage from day 1, but did not share parentage. Chicks that share the same parents might have inherited genetic preferences for vegetation (or configuration of vegetation). Chicks were maintained at a room temperature of 29–31°C for the first week of life, and were fed four or five times a day with live or frozen fish (*Menidia, Ammodytes, Fundulus*).

In 1984, sibgroups were randomly divided into two treatments: one had beach grass (*Ammophila*) in the cages (three cages with four chicks each), and the other had goldenrod (*Solidago*) in the cages (three cages with four chicks each). Each cage (30 × 50 cm) had a 5-cm deep layer of sand covering the floor, and vegetation was placed at only one end forming a shelter 15 cm wide and 36 cm high. Plants were selected to be of equal height and width to provide equivalent physiognomic cues. For each species, stems were tied

TABLE 1

DISTANCE[a] OF CHICKS FROM END WITH VEGETATION

Day	Goldenrod	Grass	No vegetation	Both species of vegetation[b]
1	9 ± 1.2	11 ± 2.1	22 ± 10.1	10 ± 1.0
2	10 ± 1.5	10 ± 2.3	21 ± 9.3	7 ± 1.2
3	18 ± 1.0	9 ± 3.3	27 ± 12.1	8 ± 1.8
4	15 ± 3.1	2 ± 0.5	21 ± 13.1	7 ± 1.0
5	19 ± 2.5	13 ± 4.3	21 ± 10.3	8 ± 1.2
6	1 ± 0.5	7 ± 3.1	23 ± 12.1	6 ± 0.1
7	2 ± 0.5	16 ± 2.0	18 ± 9.3	4 ± 0.1
8	2 ± 0.5	15 ± 3.1	23 ± 13.7	3 ± 0.8

[a] Mean ± SE in cm.
[b] Goldenrod at one end, grass at the other. Measurements are from the end chicks were closest to.

together at the base to insure similar appearance. In 1986 the sibgroups were randomly divided into two treatments: one had no vegetation (three cages with four chicks each), and the other had beach grass at one end and goldenrod at the other end (four cages with four chicks each), otherwise cage size and substrate were similar. The long axis of the cage was divided into equal sections from 0 at one end (under vegetation in three tests) to 6 at the opposite end to facilitate recording the location of chicks.

Beginning on the first day of captivity, for eight days we recorded the location of each chick at 0600, 1000, 1400, and 1800 (except on day 8) using a spot scan. On day 8 and 9 chicks were tested for vegetation preferences since this is the time when they begin to move around in nature.

On day 8 each chick was placed in the center of a test chamber (100 cm long × 25 cm wide × 40 cm high) with an *Ammophila* plant at one end and a *Solidago* at the other end. Chicks were allowed 2 min to move towards one or the other end before we recorded their position. Later in the day chicks were again placed in the test chamber and were startled by the sudden approach, from above, of an unfamiliar person dressed in a bright red shirt. We then recorded the chicks' location at 15, 30, 45, and 60 sec. On day 9 we repeated the experiment, reversing the location of the vegetation types.

We calculated Goodness of Fit tests with Yates corrections, yielding χ^2 to determine differences (Sokal and Rohlf 1981), using a hand-held calculator.

Results.—Common Tern chicks raised with vegetation normally remained near the vegetation in their rearing cages, seldom moving more than 20 cm from it (Table 1). Initially chicks remained about 18–20 cm from the base of the vegetation. In all experiments each chick's location was noted four times a day for eight days (except for the 1800 census on day 8, N = 31). For all cages with vegetation each chick was within 25 cm of the vegetation on at least 29 of the censuses, indicating a clear preference for the vegetation. No such distribution was obvious for chicks in cages without vegetation. During the eight days, chicks in cages with only goldenrod eventually moved directly under the vegetation whereas chicks in cages with only grass remained near, but not under it and showed no clear daily change in location. Thus when undisturbed in their natal cages, tern chicks with only one plant remained near it, and those near goldenrod moved under it when they were older. Chicks raised with two plants initially stood near the middle and later moved to one or the other plants. Chicks raised in cages without plants moved about the cage. Some did not remain

TABLE 2

RESPONSE (CELL COUNTS) OF COMMON TERN CHICKS WHEN DISTURBED AND UNDISTURBED[a]

Response	Natal habitat			
	Goldenrod	Grass	No vegetation	Both species vegetation
Undisturbed				
Goldenrod	58 (7)	42 (5)	2 (3)	44 (7)
Grass	42 (5)	58 (7)	25 (3)	31 (5)
None	(0)	(0)	50 (6)	25 (4)
Disturbed				
Goldenrod	92 (11)	8 (1)	19 (2)	19 (3)
Grass	8 (1)	92 (11)	19 (2)	62 (10)
None	(0)	(0)	62 (8)	19 (3)

[a] Chicks were tested only once when undisturbed and once when disturbed.

consistently in any one spot (variable mean and large standard error, Table 1); others consistently leaned against one side of the box.

When placed in a test chamber, chicks from all four treatments showed no significant preference for vegetation species when not frightened (Table 2, χ^2 test with Yates correction <4.40, df = 1 not significant, Sokal and Rohlf 1981). Chicks often walked to one vegetation type, and then walked to the other, looking around. They usually stood next to vegetation after 1 min, but they did not hide under it. Some chicks raised with both or neither plant did not move close to vegetation during the test. When tested in a relaxed situation chicks raised with one plant species were consistent in their responses from the first to the second test, whereas those raised with both or neither plant species were not (χ^2 with Yates correction = 8.1, df = 1, $P < 0.01$).

When exposed to a startling stimulus, there was a difference among groups in the proportion of birds responding (χ^2 with Yates correction = 15.4, df = 3, $P < 0.001$), and in their response (χ^2 with Yates correction = 21.9, df = 1, $P < 0.001$). All birds raised with only one plant species responded, but only 67% of the chicks raised with neither or both plant species in their cages responded. Chicks raised with only one plant species showed a significant preference for their natal vegetation ($\chi^2 = 8.24$, df = 1, $P < 0.001$, Table 2). Most chicks immediately ran, without hesitation, to their natal vegetation and scurried under it, often disappearing from view. After 20 or 30 seconds chicks sometimes walked to the edge of the vegetation and peered about. When exposed to a startling stimulus 81% of chicks raised in cages with both plants also ran to vegetation but showed no significant preference for grass or goldenrod, and no tendency to move toward the vegetation they had preferred in the cage.

Discussion.—In mammals and birds heredity as well as experience appears to play a role in habitat preference (Wecker 1963) and presumably in selection of shelter sites. Partridge (1974) showed that naive tits (*Parus ater, P. caeruleus*) raised in cages devoid of vegetation preferred the type of tree in which they were most often found in the wild. However, chicks were not given a choice of trees found in the wild. In our study tern chicks, normally exposed to different species of plants in nature, were given a choice of the common natural species.

In this study Common Tern chicks from 1–8 days of age preferred to remain near vegetation. Chicks raised in cages with goldenrod moved under it while those raised in grass did

not, and chicks raised with a choice of both plants preferred goldenrod when they were in their cages. Chicks raised with no vegetation moved around the whole cage. The difference in vegetation preference may be due to the structure of the vegetation. In nature both vegetation types provide cover and protection, and we duplicated this in the laboratory. However, goldenrod provides more room under the leaves, and because the leaves are broader the chicks could peer out between them. *Ammophila* grass has many more stems, and sometimes does not provide an open place under it for all siblings to hide.

When startled, chicks raised with either plant species alone immediately ran to their natal vegetation, and moved easily under the leaves, whereas those raised with both plants ran to vegetation but showed no clear preference. Chicks raised with both or neither plants showed no preference for either plant species when tested in a relaxed atmosphere or when startled. This indicated that the plants we used for our tests were equally attractive. We concluded that the preferences shown by chicks raised with only one species, but tested with both, were the result of their early experience.

In nature, chicks could be warned of danger by calls of parents, or by the behavior of other chicks, or by the dangerous stimulus itself. In any case it would be adaptive for young chicks to hide quickly under cover. Moving to familiar vegetation has several advantages: (1) quick and rapid choice with a minimum of delay, (2) assurance that there is room to hide, and (3) increased likelihood that only siblings will be under that particular bush. If other non-sibling chicks are present, particularly larger ones, the escaping chick may be forced out into the open sand and danger. Our study, in contrast to others, showed a temporal increase in preference for the natal vegetation (for chicks raised with goldenrod), and a preference for their natal vegetation when offered a choice between two plants found in nature. Since chicks raised with only one plant ran to it when startled, but chicks raised with both plants or no plants showed no clear preference for plant species when startled, we conclude that experience rather than innate preferences obtain. These results thus extend previous studies in documenting the role of experience in temporary habitat choices.

Taken together, the results of these experiments indicate that chicks prefer to remain near cover, and select a familiar vegetation type when startled. Strong vegetation affinity developed early, enabling chicks to find quickly familiar cover when startled or threatened by predators or conspecifics, increasing their overall survival. These preferences and abilities develop in the first week of life.

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Brood adoption and apparent infanticide in a north-temperate House Wren population.— In many bird species, a mate who dies or deserts during a breeding attempt may be replaced by another bird before the breeding attempt terminates. Replacement can also occur after physical eviction of one member of a pair by an unpaired floating bird (i.e., Freed 1986, Arcese 1989). "Replacement mates" may respond to eggs or young of the previous mate by killing them (infanticide), providing them with some form of parental care (brood adoption), or ignoring them (indifference). Rohwer (1986) reviewed the distribution of these behaviors among replacement mates in 26 species of birds. Additional cases of infanticide (among non-cooperatively breeding species) have now been reported in the Little Egret (*Egretta garzetta*), Palestine Sunbird (*Nectarinia osea*), Tristram's Grackle (*Onychognathus tristramii*), and the Barn Swallow (*Hirundo rustica*) (Fujioka 1986, Goldstein et al. 1986, Hofshi et al. 1987, Møller 1988). Brood adoption has been reported in the Black-capped Chickadee (*Parus atricapillus*), and Black-billed Magpie (*Pica pica*) (Howitz 1986, Buitron 1988). Bowman and Bird (1987) found indifference to broods among replacement mates in American Kestrels (*Falco sparverius*). In tropical House Wrens (*Troglodytes aedon inquietus*) and Tree Swallows (*Tachycineta bicolor*), replacement mates may either kill young or show indifference to broods (Freed 1986, Robertson and Stutchbury 1988). We report here on a case of brood adoption and a case of apparent infanticide by replacement males in a north-temperate

population of House Wrens (*T. aedon*). Our observations were made on the Helen Brinton Bird Reserve at the Quarter-circle A Ranch and the Reverse E4 Ranch, both near Big Horn, Sheridan County, Wyoming.

Brood adoption occurred on the territory of a color-banded male, BG, and his unbanded mate in 1987. Normal incubation stage behavior was observed by both birds at their natural cavity nest site on 4 July. On 6 July, BG was absent, and we observed a color-banded male, VS, courting BG's female at the nest entrance. VS's prior breeding history was not known. From 7–12 July, VS continued to court BG's female. On 14 July, VS carried food to the nest four times in 34 min. We observed this pair for 20 min on each of seven days from 16 to 28 July. The male and female made 20 and 29 trips to feed young, respectively. Neither adults or young were visible at the nest site on 29 July and we presume the brood fledged. This would have been one of the latest fledgings that season, and it is extremely unlikely that VS and the female made another breeding attempt that year. We do not know if VS and that same unbanded female bred together the following year.

We suspect that infanticide occurred on the territory of color-banded male YJ and his unbanded mate in 1985. The female began egg-laying on 18 June. YJ was last observed on the territory on 1 July. His mate was incubating seven eggs this day and continued to do so after YJ disappeared. On 4 July, we observed an unbanded male singing vigorously from the perch of YJ's nest box and courting YJ's female when she left the box. The nest contained seven warm eggs. On 5 July, the unbanded male continued vigorous singing and courtship. The female left the box after unusually short periods of time. She was also panting, although it was not unusually hot, suggesting that she was stressed. Five eggs remained in her nest. On 6 July, only two eggs were present, and one egg had a hole, 2–3 mm in diameter in the shell. On 7 July, the female was present but no eggs were in the otherwise undisturbed nest. She was not present on 8 and 9 July. The male removed the lining of the nest and continued to advertise for a mate on each of these days. On 10 July, the male paired with an unbanded female, and they proceeded to nest in YJ's former nest box. We do not know if this was YJ's original female. This pair made the last of the 21 nesting attempts that we followed in 1985.

While we suspect that the unbanded male destroyed the eggs in YJ's nest, two alternative explanations are possible. First, the eggs may have been taken by a predator. We consider this unlikely because in nearly all cases of nest predation the nest lining is disturbed and/or all eggs are removed at once (unpubl. data). Second, in her agitation, the female may have damaged the eggs herself. We have observed House Wrens remove eggs that we inadvertently damaged. However, House Wrens rarely damage their own eggs (pers. obs.) and it seems unlikely that the female would have damaged all seven eggs herself.

Selection should favor replacement mates who respond to eggs or young of a previous mate in a manner which maximizes their own reproductive success. Rohwer (1986) argued that for male replacements, infanticide would be favored when: (1) unpaired females are available in the population, (2) females do not normally disperse after nest-failure, (3) mate retention between seasons is uncommon, (4) desertion of one mate by another often occurs before a brood has reached independence, and (5) time remains in the season to complete only one breeding attempt [see Rohwer (1986) for a more detailed discussion]. In our population, pair bonds are formed throughout the first 10 weeks of the breeding season which indicates that unpaired females are available long after initial breeding attempts commence in very early May. We have no data, however, on dispersal after nest failure, between-season mate retention or desertion of mates by females in our population. Other studies of temperate House Wren populations indicate that the frequency of between-season mate retention is probably low. Kendeigh (1941) reported that 13–22% of pairs represented rematings from the previous season in Ohio. Drilling and Thompson (1988) found that less

than 1% of birds remated in successive seasons among House Wrens in Illinois. Kendeigh (1941) also observed frequent desertion of mates by females during the nestling stage (also see Burns 1983). In conclusion, these data suggest that selection should favor infanticidal behavior in replacement male House Wrens. Furthermore, the two cases of mate replacement reported here occurred late in the season when time remained to complete only one breeding attempt. This would further favor infanticide unless individuals in our population normally re-form pair bonds with their last mate from the previous season, in which case adoption may be favored.

We have too few data to determine whether selection has molded the behavior of replacement male House Wrens in our population. However, there is evidence for selection in the behavior of replacement mates in one tropical population of House Wrens. Freed (1986) has studied a Panamanian population in which mate replacement occurs in 13% of all breeding attempts. Replacements apparently kill dependent young in about 70% of cases. No evidence of brood adoption was found where young were not killed. In Freed's population, apparently few unpaired birds are available after breeding begins (also see Freed 1987), between-season mate retention is high, and the breeding season is long (up to three broods may be raised per season). Although none of these conditions specifically favors infanticide, Freed (1986) did find that dispersal by females after nest failure is rare (only 9% of females deserted territories). Selection for infanticide should be strong when there is a high probability that a prospective mate will remain on the territory after a failed breeding attempt.

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Determinacy of clutch size in Horned and Pied-billed grebes.—Clutch size of altricial birds generally is presumed to be limited by the ability of parents to provide adequate food for nestlings (Lack 1947, Klomp 1970; but see Nur 1986). Factors determining clutch size in precocial birds are more obscure (Winkler and Walters 1983), but the ability of females to produce eggs is thought to be important for many species, especially those with self-feeding young (e.g., Anseriformes; Lack 1967, Ankney and Afton 1988; but see Rohwer 1988). Many researchers have suggested that egg-production costs might also be important for birds with parentally fed young (e.g., Houston et al. 1983, Alisauskas and Ankney 1985, Hails and Turner 1985). The egg-production hypothesis predicts that observed clutch size is smaller than the most productive brood size due to the inability of females to produce additional eggs. However, some species with parentally fed young produce larger than normal clutches when eggs are removed from their nests during laying (reviewed in Klomp 1970; see also Reid 1987, Beukeboom et al. 1988). Such examples of extended egg laying do not support the egg-production hypothesis (Klomp 1970, Rohwer 1986).

Little research has focused on the factors influencing clutch size in grebes (Podicipediformes). McAllister (1958) removed one freshly laid egg (second-, third-, or fourth-laid) from each of 32 Eared Grebe (*Podiceps nigricollis*) nests. Grebes with removal nests produced an average of 3.97 eggs, versus 3.40 for 106 control nests (t-test, $P < 0.01$). Fugle and Rothstein (1977) removed all freshly laid eggs from two Pied-billed Grebe (*Podilymbus podiceps*) nests that they visited daily, beginning with the second- or third-laid eggs. One grebe produced a super-normal clutch of 13 eggs, and the other grebe laid a "normal" clutch of seven. In the present study, I conducted egg-removal and egg-addition experiments with Horned Grebes (*Podiceps auritus*) and a larger sample of Pied-billed Grebes.

Grebes were studied in 1987 and 1988 on small wetlands located near Minnedosa, Manitoba (50°10′N, 99°47′W). Egg-removal experiments involved the removal of eggs 3–6 (5

TABLE 1

MEAN NUMBER OF EGGS LAID BY HORNED AND PIED-BILLED GREBES IN RESPONSE TO EXPERIMENTAL REMOVAL AND ADDITION OF EGGS

Species:	Treatment		
	Four egg removal	Control	Four egg addition
Horned Grebe	8.60 ± 0.89 (5)[a]	6.45 ± 1.63 (11)	6.00 (1)
Pied-billed Grebe	8.14 ± 0.90 (7)	7.33 ± 1.28 (21)	7.50 ± 0.71 (2)
Combined[b]	8.33 ± 0.89 (12)	7.02 ± 1.42 (32)	7.00 ± 1.00 (3)

[a] $\bar{x}$ ± 1 SD (N).
[b] Weighted means.

nests) or 4–7 (11 nests) on the day of laying (e.g., four total eggs were removed from each nest over a 4-, or occasionally 5-, day period). Egg additions involved adding four fresh eggs to nests on days 3 and 4 of egg laying (two eggs were added each day). Controls were nests found during egg laying which were not manipulated. Clutch size represents the total number of eggs laid by the attendant female (i.e., it includes egg-removals but not egg-additions). Clutch size was recorded after laying had ceased for two consecutive days, provided nests were still being incubated. Clutch size data were analyzed using a two-way ANOVA with species and clutch manipulation as main effects (Horned and Pied-billed grebe data were analyzed together due to low sample sizes). Statistical significance was inferred based on Type III Sums-of-Squares (SAS Institute Inc. 1985).

Mean clutch sizes for control nests were 6.5 for Horned Grebes and 7.3 for Pied-billed Grebes (Table 1); this difference was not significant($P_{(\text{species effect})} = 0.17$), although other studies from this area indicate that Pied-billed Grebes lay slightly larger clutches than do Horned Grebes (Sealy 1978, Ferguson and Sealy 1983). Egg removal had a significant influence on total number of eggs laid ($P_{(\text{treatment effect})} = 0.007$), with removal birds laying, on average, 1.3 more eggs than did controls. This effect did not differ statistically between Horned Grebes and Pied-billed Grebes ($P_{(\text{interaction effect})} = 0.28$), although inspection of the data suggests that Horned Grebes may have been more responsive to removals. Few egg-addition nests were obtained; the three nests which reached incubation stage contained normal numbers of host eggs (Table 1).

Horned and Pied-billed grebes did not meet Cole's (1917) definition of indeterminate layers; they did not suspend laying in response to egg-additions and they did not completely compensate for the four eggs removed during removal experiments. Neither did Horned and Pied-billed grebes meet Cole's definition of determinate layers; removal birds laid significantly more eggs than did control birds. These results, like previous studies (McAllister 1958, Fugle and Rothstein 1977), provide ambiguous evidence for the egg-production hypothesis. Some individuals were clearly capable of producing more eggs than normal, thus egg-formation costs would not appear to be constraining clutch size in these individuals. However, some individuals did not respond to removals by producing additional eggs. This may indicate that they were unable to produce additional eggs, or it may indicate only that birds did not receive the proper stimuli nccesary to extend egg laying (Klomp 1970, Winkler and Walters 1983, Rohwer 1986).

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Wax-eating by African Common Bulbuls.—Recent evidence (Obst, Wilson Bull. 98:189–195, 1986; Roby, Place, and Ricklefs, J. Exp. Zool. 238:29–41, 1986) indicates that some and perhaps many seabirds depend upon a substantial amount of wax in their diet. Honeyguides (Indicatoridae) long have been known to eat wax regularly, using beeswax, or in some cases, the waxy exudate of scale insects as food (Friedmann, Bull. U.S. Nat. Mus. no. 208, 1955; Reyer and Isack, Science 243:1343–1346, 1989). There have been few investigations into the actual digestion of wax (Friedmann and Kern, Can. J. Microbiol. 2:515–517, 1956; Obst, Wilson Bull. 98:189–195, 1986; Diamond and Place, Ibis 130:558–561, 1988). It is known, however, that Greater Honeyguides (*Indicator indicator*) can live for three or more months exclusively on a diet of beeswax (H. A. Isack, pers. comm.).

Our Kenyan field studies of honeyguides rely upon a beeswax "feeding station," an old beehive cut out years ago by honey-hunting tribesman, having various crevices and wired trays into which we put wax. The beeswax is supplied ad libitum in more or less pure form (impure wax with particles of bees or dead bees and debris does not keep well under field conditions). Our studies are conducted on the Gallmann Memorial Foundation's Ol Ari Nyiro Ranch at 1800 m on the Laikipia Plateau, 25 km east of Lake Baringo in central Kenya.

While observing five to 38 individual honeyguides of up to four species (Short and Horne, Amer. Mus. Novitates no. 2825, 1985) feeding daily at the wax feeder, we have noted various other birds (and mammals such as squirrels, as well as skinks) that sporadically come to the feeder and eat bits of wax. Such birds are: Yellow-spotted Petronia (*Petronia pyrgita*), Chestnut Weaver (*Ploceus rubiginosus*), Red-cheeked Cordon-bleu (*Uraeginthus bengalus*), African Black-headed Oriole (*Oriolus larvatus*), and Common Bulbul (*Pycnonotus barbatus*). We have had five to 20 observations of each of these feeding on beeswax, except for the Common Bulbul which feeds on it much more frequently. In three August to November field seasons (1985 to 1987), at least one such bulbul briefly visited a hive feeder, poked into the wax, and took at least one piece about every second day. However, from July to October 1986 up to five Common Bulbuls sporadically, and then more regularly, visited and fed at the hive feeder; two became daily visitors. One of these individuals, which could be distinguished by heavy yellow pollen matted on the feathers of its forehead and front of its crest, developed a strong wax-eating habit. Bulbuls in the area were paired at the time, and no more than two visited the hive at once. Only the bulbul that became more persistent in its wax-feeding consistently had matted yellow pollen on its head (others showed a yellow spot or two occasionally), and it usually was accompanied at the hive by its presumed mate that lacked the yellow color. Although we could not identify with certainty all the bulbuls visiting the wax-feeder (we were reluctant to net them for fear of affecting the honeyguide research), we could distinguish the heavily pollen-marked individual and its mate from neighboring pairs of bulbuls. This particular pair actively defended a territory including the area within 10 m of the wax-feeder, driving off the other bulbuls. Thus, we were able to document the increase in attendance of the pollen-marked bulbul and its apparent mate at the wax-feeder (Table 1).

The presence or absence of honeyguides about the feeder, the presence or absence of different honeyguide species, and the dominants vs subordinate feeding honeyguides affected visits of the bulbuls to the feeder. When larger honeyguides, the Greater and Scaly-throated (*I. variegatus*), were present and interacting in numbers, the bulbuls approached but then flew off without going to the feeder. When only one or two larger honeyguides, and especially subordinate ones (to other conspecifics) were present, the bulbuls came in and often sup-

TABLE 1

SUMMARY OF COMMON BULBUL OBSERVATIONS AT WAX FEEDER IN 1986

Date	No. of individuals visiting[a]	Min of observation	Actual no. of visits	Min with bulbuls at hive
27 August	1 (?)	130	1	4
28 August	2 (2)	180	1	5
30 August	3 (2)	300	6	24
1 September	2 (2)	210	2	9
3 September	2 (2)	180	5	23
5 September	2 (2)	180	3	15
7 September	2 (?)	100	4	21
11 September	2 (2)	150	2	25
13 September	2 (2)	120	3	14
15 September	2 (2)	180	4	30
21 September	2 (2)	350	5	188
23 September	1 (1)	120	4	30
26 September	2 (2)	150	3	45
28 September	3 (2)	130	4	67[b]
30 September	2 (2)	180	4	30
2 October	2 (2)	210	7	118[b]
4 October	2 (2)	200	13	91[b]

[a] In parentheses we indicate the numbers of the pair including the chief feeding bulbul.
[b] Time spent greater than that of any honeyguide on that day.

planted them. When Lesser Honeyguides (*I. minor*), much smaller than the bulbuls, were present singly or in any numbers, the bulbuls went directly to the feeder and drove them off. In fact, the frequently visiting pair of bulbuls gradually became very aggressive to Lesser Honeyguides (juveniles of which, despite their small size, ordinarily were dominant to the larger honeyguides). More and more the activity of the bulbul pair centered about the feeder, and by October the chief wax-eating bulbul frequently perched for long periods near the feeder, and vigorously chased away every incoming Lesser Honeyguide. On 4 October 1986, we collected this wax-eating bulbul after it had been feeding uninterruptedly on wax for 35 min (in addition to feeding on wax earlier in the day). It proved to be a male with slightly enlarged testes. Its stomach was crammed with soft, "milky" wax like that found in the stomachs of honeyguides, although slightly more solid in form and perhaps less digested. No other food items were detected in its stomach. Since our removal of this individual, no other bulbul subsequently has taken up this unusual habit, although bulbuls frequently pass about the hive, perch on it, or even occasionally peck once or twice at the wax, eating some.

We used various forms of beeswax, including "pure" wax on many days, but found no indication that the bulbuls were selecting conspicuous non-wax items such as parts of bee larvae. We conclude that the chief wax-feeding bulbul was eating wax. As B.S. Obst had noted to us (in litt.), beeswax, even in pure form, contains wax esters, complex hydrocarbons and other organic compounds, so the "wax" contains sources of energy stored in wax-ester and non-wax form. What elements of the beeswax were being utilized by the bulbul, and how it was able to digest them are unknown. What is certain is that this particular bulbul was selecting and feeding extensively on beeswax, and even was defending the wax source against other birds. These observations imply that it was indeed securing nutrients from the

wax. The long period over which the bulbul fed on wax suggests that it encountered no problems in using a food item undigestible to most animals. The honeyguide-bulbul interactions also suggest the obstacles presented by honeyguides in the possible evolution of beeswax-eating habits by other birds in the range (Asia, Africa) of honeyguides.

When bulbuls came to the feeder after honeyguides had been feeding we noted that the bulbuls usually went directly to the particular site that the honeyguides had vacated. Possibly the bulbuls could have acquired some capability to digest wax from wax pieces that had been "mouthed" by, or disgorged by honeyguides, if digestion of wax esters occurs by microbial fermentation, as suggested by Friedmann and Kern (1956; but see Roby et al. 1986, who discuss wax digestion by enzymatic hydrolysis).

Our observations suggest that landbirds other than honeyguides have, or can develop, the ability to utilize beeswax, and we agree with Diamond and Place that many birds may have the capacity to digest wax.

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The effect of observer variability on the MacArthur foliage density estimate.—Scientists have used the technique developed by MacArthur and MacArthur (1961) for many years to estimate shrub and tree foliage density during studies of avian-habitat relationships (MacArthur et al. 1966, Recher 1969, Willson and Moriarty 1976, Dickson and Segelquist 1979, Conner et al. 1983). Conner and O'Halloran (1986) compared the accuracy of estimates made using the MacArthur technique with actual leaf surface area and biomass. They determined that the MacArthur and MacArthur (1961) technique provided an excellent relative estimate of the surface area and biomass of foliage and supported its use to measure foliage in avian-habitat studies. Although Conner and O'Halloran (1986) suggested correction factors to adjust the technique to provide more exact estimates of leaf surface area, they did not examine an important potential bias of the technique. Because the technique requires an observer to estimate when 50 percent of a black-and-white checkered board is obscured by foliage, the comparability of studies by different researchers is in question. The experience of an observer in estimating how much the density board is obscured also has the potential to affect variability and accuracy of foliage estimates.

Observer differences can affect foliage density estimates in two major ways. First, the basic accuracy of the estimation is at question; how close is the observer's estimate to the desired 50 percent obscurity of the black-and-white checkered density board? Second, how consistent is the observer in making estimations?

Methods.—A basic problem with comparing the accuracy and abilities of different observers is damage to the vegetation because of repeated measurements made at each test location. To avoid this problem a series of photographs (100) was taken of a black-and-white checkered density board. Each photograph (12.7 × 17.7 cm) was taken at a different location with varying proportions of the density board obscured by foliage. Thirteen of the

TABLE 1

COMPARISONS OF OBSERVER ESTIMATES OF FOLIAGE OBSCURITY OF A BLACK-AND-WHITE CHECKERED DENSITY BOARD

Foliage estimator	Average percentage obscured	Standard deviation	Coefficient of variation (%)	Correlation to actual (*r*)
1 (Actual)	50.6	15.8	24.9	1.00
2 (Random)	51.3	28.0	78.6	0.22
3	55.2	17.5	30.5	0.59
4	71.0[a]	20.4	41.7	0.68
5[b]	54.3	15.1	22.9	0.85
6[b]	48.5	15.5	24.1	0.78
7[b]	52.1	14.5	21.2	0.71
8	37.0[a]	14.2	20.2	0.58
9	42.3[a]	14.3	20.5	0.83
10	38.4[a]	17.3	29.8	0.69
11	61.6[a]	18.3	33.5	0.79
12	70.7[a]	16.7	27.8	0.76
13	70.4[a]	18.3	33.6	0.86
14	45.5	15.3	23.3	0.85
15	40.1[a]	14.3	20.6	0.82
16	31.8[a]	13.8	18.9	0.72
17[b]	51.5	15.9	25.3	0.64
18	48.5	13.2	17.5	0.72
19	43.0[a]	13.8	19.1	0.77
20	50.3	18.0	32.3	0.78
21	46.6	16.2	26.1	0.74
22	72.7[a]	14.7	21.6	0.69
23	52.6	15.5	23.9	0.84

[a] ANOVA, Duncan's New Multiple Range Test, $P < 0.05$.
[b] Experienced observer (observers 3, 4, 8–16, and 18–23 were inexperienced).

photographs contained only pine foliage, 55 only deciduous foliage, and 32 varying mixtures of pine and deciduous foliage. All photographs were taken in young pine plantations in Nacogdoches County, eastern Texas. The square density board was positioned so that its center was 1 m above the ground and photographs were taken with the camera lens also 1 m above the ground. Surface area of the density board was 0.5 m^2.

The percentage of the checkered density board that was actually obscured by foliage was measured on each photograph with a dot grid matrix (9 dots/cm^2) as described by Conner and O'Halloran (1986). Twenty-one individuals examined each of the 100 photographs and estimated the percentage of the checkered density board that was obscured by foliage. Four of the observers were experienced with the MacArthur method, while the other 17 were not. In addition to the percentage estimates made by the 21 observers, a random numbers table (Rohlf and Sokal 1969) was used to randomly select a value ranging between 1 and 99 percent for each photograph as a random estimate of percentage of the board obscured by foliage.

Means and standard deviations for all observers and the random values were compared with actual foliage obscurity determined by using the dot grid matrix. Pearson correlations of actual foliage percentages with each observer's estimates were calculated.

Results.—All observer estimates of the percentage that foliage obscured the black-and-white checkered density board were significantly correlated (Pearson correlation, $P < 0.001$) with the actual obscurity as measured by the dot grid matrix. Although random obscurity values were also correlated to the actual measures, the magnitude of significance was lower ($P = 0.013$, Table 1). The average correlation of estimates by the four experienced observers with actual foliage was $r = 0.75$ and inexperienced observers also averaged $r = 0.75$.

The coefficient of variation (CV) for random foliage values (78.6) was much greater than CVs for the actual foliage present or any of the 21 observer estimates (Table 1). Experienced observers had a slightly lower average CV (CV = 29.6) than did nonexperienced observers (CV = 32.3), but estimates of experienced observers were not significantly different from inexperienced observers (ANOVA, $P > 0.10$).

Estimates of 11 observers were significantly different from the actual foliage values (ANOVA, Duncan's New Multiple Range Test, $P < 0.05$, Table 1). Six observers consistently estimated percentages lower than the actual percentages, while five observers estimated consistently higher percentages. The foliage estimates of 10 observers (all four experienced observers plus six inexperienced observers) were not significantly different from the actual foliage present.

Discussion.—All observer estimates were very highly correlated with actual foliage values, indicating that relative differences in foliage estimates within each separate research study should be reliable. This agrees with the observations of Conner and O'Halloran (1986). Comparability between studies might be increased if only experienced observers are used to collect data used in research studies. Training for field personnel that provides feedback on accuracy of foliage estimates (direction and percentage deviation from actual foliage obscurity) should be considered.

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Diet of Gurney's Buzzard in the Puna of Northernmost Chile.—Gurney's, or Red-naped, Buzzard (*Buteo poecilochrous*), is confined to the Puna zone at elevations above 3500 m along the Andean range, from Colombia south through Ecuador and Peru, to northernmost Chile and adjacent regions of Bolivia and Argentina (Vaurie 1962, Brown and Amadon 1968). According to Johnson (1965) "Very little is known of its habits," except for scant behavioral information reported on a pair breeding in southwestern Peru (Johnson 1967). Little is known about its population status (Jaksić and Jiménez 1986), and we found no studies of its diet in the specialized literature. Herein we report quantitative information on the diet of Gurney's Buzzard in the high Andean plateau (Puna) of northernmost Chile.

On 1 March 1988 we found a recently abandoned nest of Gurney's Buzzard (some of its feathers were inside) on a cliff ca 4800 m elevation at Choquelimpie (18°19′S, 69°18′W, see Paynter 1988 for more information on this locality). The date corresponds to the end of both the breeding season and the warm/rainy season in the Puna, when air temperatures average 12°C. The vegetation is that of a cold steppe dominated by dwarf shrubs (e.g., *Adesmia spinosissima, Baccharis incarum*) and bunchgrasses (e.g., *Festuca orthopylla, Stipa* sp.). In areas where the watertable emerges, swampy vegetation prevails, dominated by cushion plants (e.g., *Distichia muscoides, Oxychloe andina*). We collected regurgitated pellets below the nest and prey remains from inside it. The state of pellets and of remains implied that they represent the diet of Gurney's Buzzard during the breeding season. We analyzed pellets using standard procedures described by Marti (1987). To gauge prey contents against prey availability in the field, we recorded the presence of all vertebrates in the area. We collected anurans by hand, lizards by snaring, and small mammals by trapping. We assessed small mammal abundance with an average of 150 medium-sized Sherman traps, operated for five nights, totalling 800 trap-nights, and with three gopher coil spring traps, operated during two nights.

Mammals made up a numerically small part of the diet of Gurney's Buzzard (Table 1). The only instance of carrion consumption was represented by the hooves of either a domestic goat or a sheep found among nest remains. All other prey likely was taken alive. By live-trapping we collected 16 rodents of five species in the area: eight Puna vesper-mouse (*Calomys cf. sorellus*), three Puna tucotuco (*Ctenomys opimus*), two Puna greater mouse (*Auliscomys sublimis*), two Leaf-eared mouse (*Phyllotis* sp.), and one White-bellied field mouse (*Akodon albiventer*). The most abundant rodent in the area (vesper mouse) was not among the prey of Gurney's Buzzard. Conversely, Tschudi's cavy (*Cavia tschudii*) and Andean field mouse (*Akodon andinus*) were among its prey but were not captured in the traps.

Birds contributed a minor component of the diet, mainly with thinocorids and fringillids (Table 1). We identified 34 species of birds in the area, among them two Tinochoridae, Gay's Seed-snipe (*Attagis gayi*) and D'orbigny's Seed-snipe (*Thinocorus orbignyianus*), and seven Fringillidae: Plumbeous Sierra-finch (*Phrygilus unicolor*), White-throated Sierra-finch (*P. erythronotus*), Ash-breasted Sierra-finch (*P. plebejus*), Grey-hooded Sierra-finch (*P. gayi*), White-winged Diuca-finch (*Diuca speculifera*), Yellow-rumped Siskin (*Carduelis uropygialis*), and Black Siskin (*C. atrata*).

Reptiles were represented in the diet only by lizards (Table 1). In the area we collected three, or possibly four, *Liolaemus* species: striped lizard (*L. alticolor*), James' lizard (*L. jamesi*), variable lizard (*L. multiformis*), and *Liolaemus* sp. (this latter may be a juvenile stage of variable lizard). Of these species, the two former were the most abundant and were represented accordingly among the Buzzard's prey. Only a single amphibian, a frog or toad, was found among prey remains in the nest (Table 1). In the area we collected the spiny toad (*Bufo spinulosus*) and two leptodactylids, rufous frog (*Pleurodema marmorata*) and Peruvian

TABLE 1

PREY OF GURNEY'S BUZZARD IN THE PUNA OF NORTHERNMOST CHILE, BASED ON PELLETS AND NEST REMAINS COLLECTED AT THE END OF THE BREEDING SEASON

Prey	Percent of individual prey	
	Pellets	Nest remains
Mammals	8.3	4.4
White-bellied field mouse	0.7	0.0
Andean field mouse	0.7	0.0
Leaf-eared mouse	0.4	0.0
Tschudi's cavy	0.4	0.0
Puna tucotuco	1.4	0.0
Cricetidae	2.5	2.2
Rodent	2.2	0.0
Goat or Sheep	0.0	2.2
Birds	4.0	2.2
Thinocoridae	0.7	0.0
Fringillidae	0.7	0.0
Passerine	1.4	0.0
Bird	1.2	2.2
Reptiles	7.6	8.9
James' lizard	4.7	8.9
Striped lizard	0.7	0.0
Liolaemus lizard	2.2	0.0
Amphibians	0.0	2.2
Anuran	0.0	2.2
Insects	80.1	82.3
Tenebrionidae	3.3	4.4
Scarabaeidae	1.8	0.0
Curculionidae	14.1	6.7
Coccinellidae	0.4	0.0
Coleoptera adult	59.4	66.8
Coleoptera larva	0.0	4.4
Hymenoptera adult	0.4	0.0
Lepidoptera larva	0.7	0.0
Total prey	276	45
Total pellets/remains	27	45

frog (*Telmatobius peruvianus*). Insects were the most frequent prey in the diet of Gurney's Buzzard, most of them being coleopterans (Table 1). Wasps and caterpillars made up a small proportion of its diet. All these insects were small, probably weighing less than 1 g, and thus their contribution to the total biomass of the diet seems negligible.

A comparison between prey in the pellets and that among nest remains (Table 1) does not reveal any significant difference between these two ways of sampling the food habits of Gurney's Buzzard. In sum, its diet numerically is dominated by insects, but by biomass it

appears that vertebrates (particularly rodents and lizards) constitute the staple prey of Gurney's Buzzard during the breeding season in the Chilean Puna.

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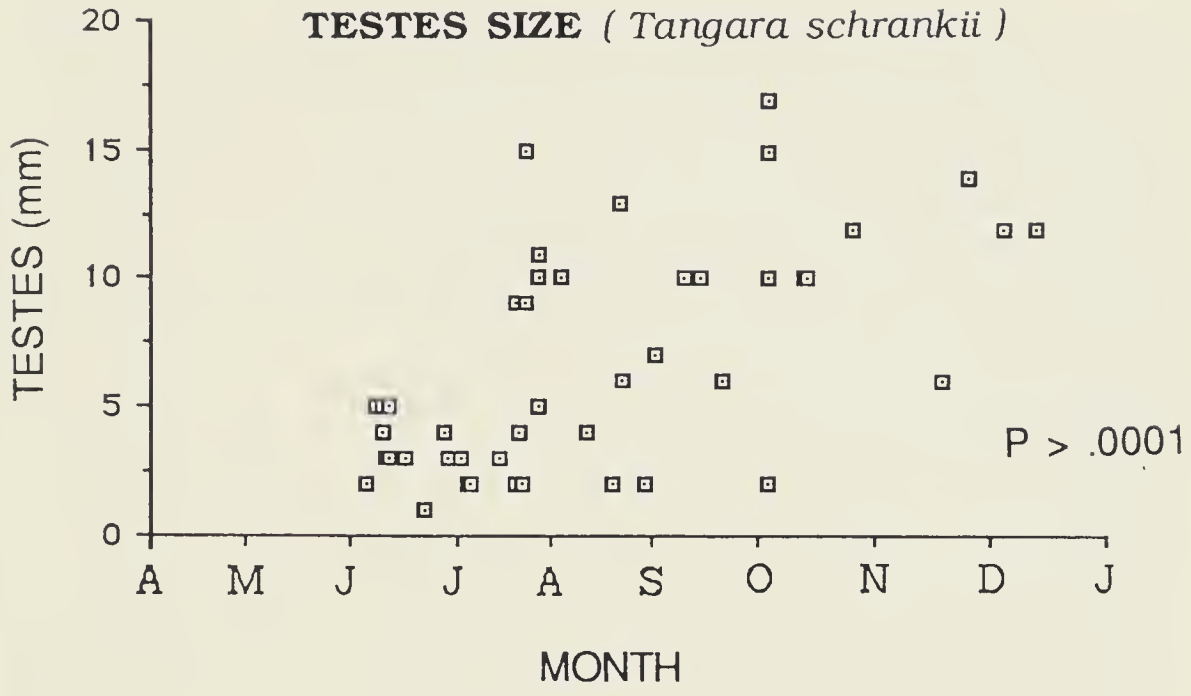
Nest, eggs, and young of the Green-and-Gold Tanager, with notes on timing of breeding.—Little or nothing is known of the breeding biology of half of the 50 species of tanagers in the genus Tangara (Isler and Isler, *The Tanagers,* Smithsonian Institution Press, Washington, D.C., 1987). One such species, the Green-and-Gold Tanager (*Tangara schrankii*), is a common bird of the canopy of terra firme rainforest in western Amazonia, from the base of the eastern Andes in s.e. Columbia south to n. Bolivia and s.w. Brazil (Isler and Isler 1987). Isler and Isler (1987) gave a brief description of a nest and eggs of *T. schrankii* found in southeastern Peru by T. S. Schulenberg. Herein, I provide a detailed description of a nest found by myself, the nest found by T. S. Schulenberg, and of a third nest found by Phyllis Isler. To investigate the timing of breeding, gonad data from specimen labels were analyzed.

In 1987, a field party from Louisiana State University Museum of Natural Science conducted an ornithological survey in a previously unexplored area of Peru ca 65 km ENE of Pucallpa, Dpto. Ucayali. On 31 July, I flushed an adult *Tangara schrankii* from an understory sapling 3 m in height in tall rainforest. On the sapling, I found a cup-shaped nest composed of and lined predominately with dried leaves, but also mixed with rootlets and lichens. It was built at the base of a branch 75 cm above the ground and concealed by an overhanging fern frond woven to the sapling. Other live and dead fronds and leaves of a *Philodendron* sp. also concealed the nest. The dimensions of the nest were 12.2 cm from top to bottom, 10.2 cm from outer side to outer side, and 6.6 cm deep. It contained two pale reddish brown eggs densely speckled with darker red. Three days later, both young had hatched. The chicks were sparsely covered in downy feathers and had a whitish gape and a Spectrum Red (Ridgway, *Color Standards and Nomenclature,* Washington D.C., 1912) mouth-lining. The adult (18 g, ovary 10 × 7 mm, oviduct 2 mm wide, and all ova under 1 mm), young and



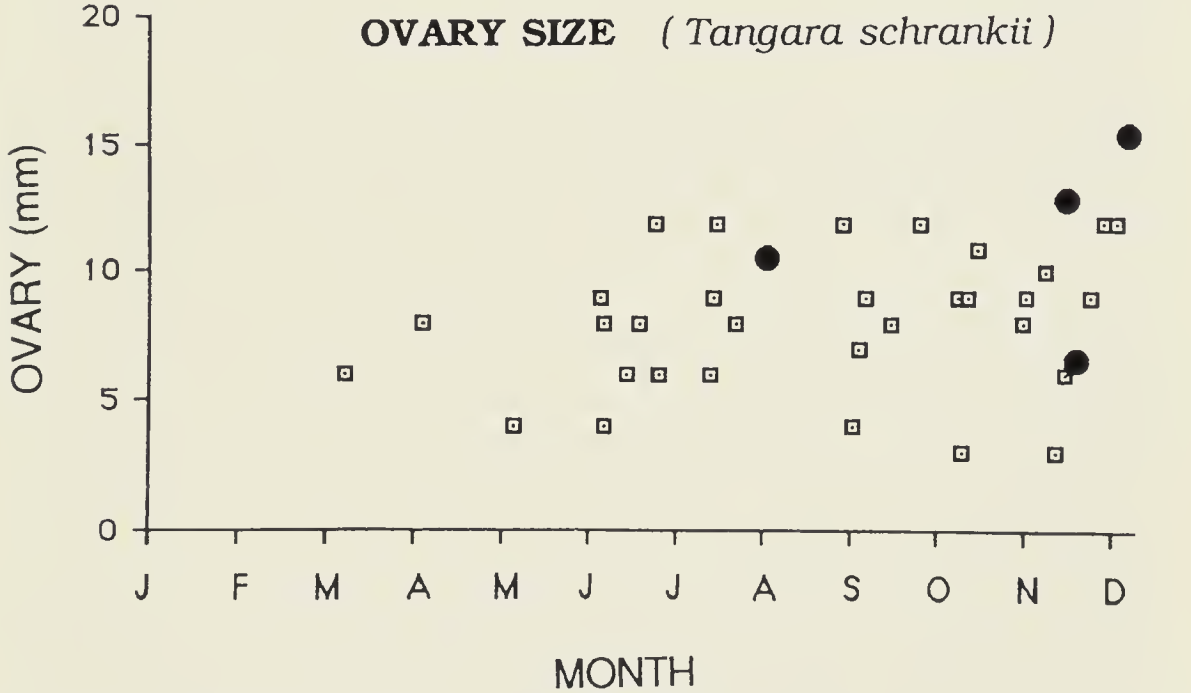


FIG. 1. Gonad data for *Tangara schrankii*. When gonad data were taken from the specimen label, the largest dimension was plotted. If testes were classified on specimen labels as "TM" (testes minute), "TSE" (testes slightly enlarged), or "TE" (testes enlarged), they were placed into "2 mm," "6 mm" and "10 mm" size categories. Ovary data noted on specimen labels with an acronym was not used. Solid circles represent enlarged ova or oviducts.

nest were collected and will be deposited in the Louisiana State Univ. Museum of Natural Science. Unfortunately, due to uncontrollable circumstances, all specimens remain in Peru and no catalog numbers are available at this time. Photographs of the nest and young have been deposited with Vireo (v06/6/001-003). The only other *Tangara* species known to construct a nest almost entirely with dried leaves is the Lesser Antillean Tanager (*T. cucullata*); the majority of known *Tangara* nests consist largely of moss (Isler and Isler 1987).

Schulenberg found a nest (Isler and Isler 1987) at the mouth of the Rio la Torre on the south bank of the Rio Tambopata, Dpto. Madre de Dios, Peru. He flushed an incubating bird on the morning of 3 August (1987) and collected the nest and eggs the following evening; they are deposited at the Museo de Javier Prado, Lima, Peru.

This nest was similar in structure to the first described, being composed mainly of dried leaves, although lined with plant fibers. It was 2 m above the ground at the base of a *Geonoma* palm frond. Fallen leaves trapped by surrounding fronds rendered the structure inconspicuous. The nest contained two eggs, similar in color to those described above; they measured 22 mm × 15 mm and 24.5 mm × 15.5 mm. That nest was 7.0 cm × 4.8 cm deep and across, and the cup measured 6.0 cm × 4.3 cm deep and across.

On 11 October, 1987 in the same general location of the Schulenberg nest, Phyllis Isler (pers. comm.) discovered an adult *Tangara schrankii* building a nest in a small sapling (d.b.h. = 5 cm) that had broken off about 1 m off the ground. The nest, which was being built near the top of the broken stump, was completely concealed by one large leaf of *Philodendron* sp. above and several smaller leaves surrounding it. The nest was built of dead leaves and vines with some additional dead leaves trapped or possibly placed around it for camouflage.

Gonad data were obtained from 116 museum specimens (Fig. 1). Although most are from Peru, a few specimens from Bolivia, Ecuador, and Columbia were included. Unfortunately, most specimens were collected between June and November, and only 6 of the 116 were from December to May. Testes increased in size from early July to early December (Fig. 1). A significant correlation (Spearman-rank, $r = 0.63$, $P = 0.0001$) was found between testis size and date during this period. Females in obvious breeding condition (enlarged ovary) were collected from 31 July to 10 December, although no obvious breeding period stands out.

In the experience of preparators (J. V. Remsen and S. W. Cardiff, unpubl. data) at the L.S.U. Museum of Natural Science, ovary size, the most frequently reported index of reproduction on most specimen labels, is not a particularly good indicator of breeding condition. The size of the largest ovum may be a better measure of reproductive condition. Unfortunately, up until 15 years ago, bird preparators noted female reproductive condition with acronyms such as "ONE," "OE," and "OSE" and others. It is not clear whether the "O" in these acronyms refers to ova or ovary. Interpretations of such label data must, therefore, be made with caution.

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The risks of avian mobbing and distraction behavior: an anecdotal review.—The adaptive value of a behavioral trait usually is assessed in terms of its costs and benefits. Although the ultimate units of interest are fitness units, proximate measures such as time and energy expenditure or risk incurred by the performer usually are used as fitness surrogates, for expediency. Time and energy expenditures are more readily quantified than risk and thus have tended to dominate discussions of the costs of behavior. In the case of antipredator behavior, however, time-energy investment may be a poorer approximation of cost than is risk (Trivers 1972). Even for species like the American Avocet (*Recurvirostra americana*), in whose breeding biology antipredator behavior seems to play a major role (Sordahl 1986), mobbing and distraction of predators consumes only a small part of the daily time budget (Gibson 1978). Risk, however, is an elusive factor. Predation is rarely observed, and injury or mortality resulting from mobbing or distraction of a predator is a very small subset of all natural predation events. Furthermore, because mobbing and distraction usually occur in a context of parental care (Shedd 1978, 1982; Sordahl 1986) and because parental care is essential for the survival of the eggs or young in virtually all birds, death or injury resulting from these behaviors is expected to be rare because parental self-sacrifice would be counter-selected (Skutch 1976, Gochfeld 1984). Most authors simply note that these behaviors appear to be risky but probably are not highly so because: (1) the performer is alert and aware of the predator, and (2) there is little contrary evidence. It is the purpose of this paper to show that the risks of mobbing and distraction, though they may be statistically small (Gochfeld 1984:353, Hennessy 1986), are not negligible (see also Curio and Regelmann 1986). I include a literature review of anecdotes describing negative outcomes for performers of these behaviors.

Review of literature.—Predators often seem reluctant to leave an area when mobbed (pers. obs.), creating a situation with potential for aggression toward vigorous mobbers. Predators have often been reported to attack their mobbers (Forbush and May 1939:102; Meinertzhagen 1959:98, 162; Cade 1962:398; Cade 1967:49; Stefanski and Falls 1972:1509; Böcking pers. comm. *in* Curio 1978:178). There are many other reports of mobbers being killed or captured by the predator (Mason 1915; Forbush 1927:109; MacIntyre 1936 *in* Watson 1977:89; Broun 1947; Meinertzhagen 1959:87, 88, 119, 162; Cade 1962:395; Wetmore 1965:439; Friemann 1975; Myers 1978; Denson 1979; Todd 1980; McCaffery 1982; Walker 1983; England 1986; Wilson 1986). Predators such as large falcons that prey on adult birds may be particularly dangerous to mob. Meinertzhagen (1959:162) noted that the Northern Hobby (*Falco subbuteo*) is intolerant of mobbing, and Burger (pers. comm. *in* Gochfeld 1984:354) saw a Peregrine Falcon (*F. peregrinus*) capture one of the Common Terns (*Sterna hirundo*) that was mobbing it over a colony. Gochfeld (1984:354) further noted that he has captured mobbing Common Terns by hand. Some predators may actually capitalize on mobbing by hunting in pairs or provoking mobbing as a hunting strategy (Smith 1969). Mobbing may be so intense that the mobber fails to see a second predator (Rudebeck 1950–51:208). Southern (1970) repeatedly observed a Northern Harrier (*Circus cyaneus*) chasing crows in a group that was mobbing a Great Horned Owl (*Bubo virginianus*), suggesting that it was trying to take advantage of their preoccupation.

Distraction behavior is probably less dangerous than mobbing, because it usually is performed at a somewhat greater distance from the predator. I found only two records of a distracting bird being killed by the predator to which it was displaying (Jourdain 1936:32, Brunton 1986). But Balda's (1965) observation of a Loggerhead Shrike (*Lanius ludovicianus*) killing a Mourning Dove (*Zenaida macroura*) that was distracting the author illustrates a dangerous property of distraction behavior—it attracts more predators than initially were

present. The circumstances of distraction display may also create significant psycho-physiological stress, even resulting in the displayer's death (Graul 1975:16, Blohm 1981).

Discussion.—The 35 examples cited above of birds being attacked, captured, killed, or dying of stress while mobbing (N = 30) or distracting (N = 5) a predator document that these behaviors are dangerous. As Hennessy (1986) pointed out, their level of danger (i.e., the probability of injury or death for an individual) relative to other behaviors is not known. Such data would be extremely difficult to obtain. However, there are other reasons to believe that mobbing and distraction are highly risky (Curio and Regelmann 1986), such as geographical variation in mobbing that is appropriate to the danger posed by local predators (Curio 1975). From a theoretical viewpoint, because the ability of many bird species to harm a predator is questionable, it may be necessary for mobbers to endanger themselves in order to "convince" the predator that their threat is real (Zahavi 1977). The threat, then, may be a sort of challenge which should often be declined because of the dissimilar benefits and costs for mobber and predator (Maynard Smith and Parker 1976, Dawkins and Krebs 1979).

The vulnerability of a mobbing or distracting bird should correlate with the distance from the predator at which the display is performed. Proximity increases the displayer's conspicuousness and the probability of eliciting an attack. An important corollary is that the effectiveness of display is probably related directly to the risk involved. It is noteworthy that distraction display practically is nonexistent in groups other than birds (Armstrong 1954:128), presumably because the risks are too high if the decoy cannot escape into an element out of the predator's reach. Even terrestrial predators such as dogs often come quite close to capturing displaying shorebirds and ducks (pers. obs.). Instances of birds distracting their avian predators are rare (Armstrong 1954:127, pers. obs.). Thus ground predators, particularly mammals, are the chief recipients of distraction behavior.

In summary, birds that mob or distract predators place themselves in close proximity to dangerous animals that may attack them. No quantitative risk assessments for individual birds have yet been made. However, I cite here 35 reports from the literature of birds being attacked or dying while mobbing or distracting a predator. Taken together, these anecdotes strongly support the hypothesis that mobbing and distracting birds are at deadly risk.

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Frequency of Northern Bobwhite X Scaled Quail hybridization.—Occurrence and plumage of Northern Bobwhite (*Colinus virginianus*) X Scaled Quail (*Callipepla squamata*) hybrids are well documented (McCabe, Auk 71:293–297, 1954; Sutton, Southwest. Nat. 8:108–111, 1963; Johnsgard, "Grouse and Quail of North America," Univ. of Nebraska Press, Lincoln, 1973). Wild hybrids are reported from three counties of the Texas rolling plains (Sutton 1963) and one county in the South Texas plains (Lehmann, "Bobwhites in the Rio Grande Plain of Texas," Texas A&M Univ. Press, College Station, 1984). Sutton (1963) suggested that interbreeding may be fairly common in portions of the rolling plains. I estimated frequency of hybridization between Texas Bobwhite (*C. virginianus texanus*) and Chestnut-bellied Scaled Quail (*C. squamata castanogastris*) in the South Texas plains.

Observations and collections are from a 4251-ha portion of the Jennings Ranch, Zapata County, Texas. In the 1986–87 hunting season, 1787 Northern Bobwhites and 257 Scaled Quail were harvested. A juvenile female hybrid (no specimen) was shot on 13 December 1986 and a juvenile male hybrid (specimen in author's possession) was shot on 16 January 1987. Thus, hybrids comprised 0.11 and 0.78% of bobwhite and Scaled Quail harvest, respectively. I trapped 433 Bobwhite and 40 Scaled Quail during October 1987, including one adult male hybrid on 5 October 1987 and two juvenile hybrids (sexes unknown) on 8 October 1987. Trapping sites of the juveniles were >1 km apart and were >3.5 km from the trapping site of the adult. I banded, photographed, and released these birds. Hybrids comprised 0.69 and 7.50% of trapped bobwhites and Scaled Quail, respectively. A juvenile male hybrid (Museum # JTK 88181) was shot on 16 January 1988. Harvest during the 1987–88 season was 1060 bobwhite and 236 Scaled Quail. Hybrids comprised 0.09 and 0.42% of bobwhite and Scaled Quail harvest, respectively.

Estimates of hybrid frequency are conservative. Deep sand sites comprise >15% of the area. Scaled Quail are absent on these sites. Excluding bobwhites trapped and harvested in

these areas would give higher hybridization rates. The boundaries I used when recording data did not follow soil boundaries and selective exclusion was not possible. I did not consider possible effects of differences in susceptibility to capture or harvest.

Interbreeding seemed to occur frequently. Captive hybrids have low reproductive capacity (Johnsgard 1973). Trials with wild stock are needed to determine the reproductive potential of hybrids of these subspecies. Genetic changes are unlikely if captive and wild hybrids have similar fertility.

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ORNITHOLOGICAL LITERATURE

LIFETIME REPRODUCTION IN BIRDS. Edited by Ian Newton. Academic Press, London, England. 1989. 479 pp. (price not known).—One of the most important developments in ornithology over the past 20 years has been the establishment of long-term studies of individual, marked birds. From such studies one can track the reproductive contribution of individuals. Lifetime reproductive success (LRS) is defined as "the total number of young raised by recognizable individuals during their lifespans," and is the theme of this book.

The volume is composed of 26 chapters contributed by more than 30 authors from many countries. Each chapter generally consists of a detailed synthesis of information accumulated during many years of study of single species. As a result, the account is very rich and extremely uneven. Chapters deal with "short-lived hole nesters" (e.g., tits [*Parus*] and other species), "short-lived open nesters," (e.g., Red-winged Blackbird [*Agelaius phoeniceus*], Indigo Bunting [*Passerina cyanea*]), "cooperative breeders," (including the Florida Scrub Jay [*Aphelocoma caerulescens*]), "birds of prey," (e.g., Osprey [*Pandion haliaetus*], Eastern Screech-Owl [*Otus asio*]), and "long-lived waterfowl and seabirds," (e.g., Barnacle Goose [*Branta leucopsis*], Short-tailed Shearwater [*Puffinus tenuirostris*]). "General issues" are discussed in two synthesis chapters.

Most chapters end with "conclusions" sections that summarize the major factors that lead to increased LRS. If all authors had followed this format, the book could be a bit more useful and editors of future syntheses would do well to insist on such conformity. In many species, lifespan was identified as the major contributor to LRS. In a few cases, environmental factors were more important. At any rate, researchers considering how to begin a long-term study will benefit from the variety of approaches used by the authors of the present volume. Obviously, techniques used to study small cavity-nesting species are not directly applicable to seabirds, but the diversity of approach here is instructive.

The book is bound in a glossy, colorful cover and appears to be highly durable. The papers are well edited and relatively free of error. However, variation in the style of figure preparation makes the chapters look more like separate scientific papers in a journal. There is a bit of confusion in the literature cited sections about whether doctoral students produce theses or dissertations. (Why cite dissertations as "unpublished?" We should be able to recognize that they are by their very nature special sorts of publications which still exist even when some of the information in them appears elsewhere.) My major complaint (and it is not so big a complaint at that) is that the editor or typesetter has changed conventional American spelling to that favored by the British (color = colour; behavior = behaviour, and the like), even in titles where the original used the former. The most egregious case occurs when Tree Swallow (*Tachycineta* [*Iridoprocne*] *bicolor*) is given as *I. bicolour*!

Perhaps the most interesting contribution of the present book is its documentation of the observation that only a few birds survive to produce young and those that do reproduce vary widely in their contributions. Individual chapters differ in their presentations of the evidence, as do the specific interests of the authors. The editor says that the aim of the book is "to bring together most of the major avian studies of lifetime reproduction. . . and find what general patterns emerge." It appears that the volume is successful in fulfilling this goal.—CHARLES R. BLEM.

WORLD BIRDBASE: THE WORLD BIRDER'S DATABASE. Santa Barbara Software Products, 1400 Dover Road, Santa Barbara, CA 93103, USA. 1988:5.25" (or 3.5") floppy disks, 76 pp. manual. U.S. $99.00 + $5.00 shipping ($10.00 for foreign sales).—The tremendous expansion in interest in birding over the past two decades has been paralleled by the pro-

liferation of personal computers and computer technology. Most birders are inveterate list-makers and computers are ideal tools to assist in this task. What is needed is an information management system so that lists can be combined and compared, additional data for individual sightings can be kept, records can be retrieved and displayed, etc. With a little ingenuity most general data management systems (e.g., *dBase IV*) can be set up to accomplish these tasks. However, since there is a finite (albeit changeable) number of taxa (usually species) of interest to the birder, one of the things that might be wanted is what birds he or she *hasn't* seen. This requires that the information management system contains the names of all species of interest; for international birders (aren't we all?) this may be in excess of 9000 species. Consistent spelling of either scientific or English names also poses a problem. A system that incorporates a list of birds of the world would be most welcome.

World BirdBase is such a package. This system, an expansion and improvement of the program BirdBase, uses the same taxonomic list as the book "Birds of the World: A Checklist," by Dr. James Clements (including recent updates). Each kind of bird is identified by Order, Family, Genus, Species, and English names as well as a taxonomic sequence number. The system focuses on two kinds of records: cumulative lists (e.g., life list, backyard list) and individual sightings of a given species. In general, the data entered after the initial setup of the system will be the individual sightings; the cumulative lists are maintained automatically. Facilities are provided for retrieval of data but not for formatting which must be done using other software. Specific aspects of the program are as follows:

The backbone of the system is the taxonomic list and all data entered into the system are keyed to these names. Because both the nomenclature and the inclusion of a species on the list are subject to change, World BirdBase permits the user to modify the list by splitting, combining, or renaming species; the only feature not easily modified is the sequence, probably the least important of the attributes. Being able to modify the master list is quite important since both the choice of names and the definition of species is subject to wide international and individual variance. World BirdBase permits the user to define his or her own personal version of things and to subsequently change it when desired. Changes to the list after the system has been in use for some time will occasionally affect individual records; in most cases, the system will take care of these automatically.

Although the major feature of the system is the management of individual sight records, when setting up the system the user must make decisions as to which cumulative lists are desired. Nine lists are automatically kept by the system: 1. A "life list", i.e., any species seen anywhere, is automatically compiled. 2–5: The second category of lists is a set of four hierarchically nested lists, envisioned by the programmers as geographically more and more restricted: COuntry, REgion, LOcale, HQme (for users in the United States this might be country, state, county, back yard). The user is free to use these in other ways but is not able to rename them. They must be used hierarchically; if a record is to apply to the LO list it *must* apply to both the CO and RE lists. 5–9: Finally, there are four Special lists that can be used in any way desired (life list of birds photographed, found dead on road, seen copulating, identified by voice, etc. etc. ctc.).

The user can initialize the system by entering logical information (presence or absence) for all species for all the lists (this functionally is accomplished by noting those species which belong on each list since the default is "no" in every case), or by entering the "life" lists as though each was a "trip". Once the system is set up, the results of each birding trip are entered. Operationally, one trip is likely to be split into several parts because the system permits only one location per "trip". This is not necessarily a problem for birders who take copious notes since their records are probably already broken down this way. Each "trip" is identified by location (this field also includes comments), date, and which lists apply. The location field is 56 characters long which doesn't provide for much detail. However, if more

detail is needed, the "trip" can be split into two or more locations, each with a 56 character name. The country of the location is entered as a two-character code. Dates can be either MM-DD-YY or DD-MM-YY depending on configuration, but the year is restricted to the period 50 (=1950) through 49 (=2049).

Entry of actual data from each "trip" involves highlighting the name of the bird on the master list, hitting the return key, entering comments (if any) and hitting the return key. This is repeated until all species on the list have been accounted for. A "trip" may involve just one species or hundreds. The system provides a sophisticated "find" utility for locating a species on the master list (as well as two different paging functions). However, the "find" utility usually starts at the beginning of the list so that jumping to species in the "higher" passerines is slow; having the data sorted in taxonomic order can speed entry. Once data have been entered, records can be deleted, and the various cumulative lists can be edited.

Information can be retrieved using several different fields, including species, date, first sighting of species, location, etc. This display utility retrieves complete records in a standard format and lists them on the screen, printer, or to a file. If the records are written to a file, two formats are available, Word Processing (as the records are written to the screen) and Data (standard double quote/comma delimiting for importation into other databases or analysis software). No other formatting is available.

World BirdBase is written for IBM-compatible personal computers and is copy-protected. A minimum of 640k RAM, one floppy disk drive, and a hard disk drive are required. The master name file takes nearly 800k. The storage of sight records is reasonably efficient: the maximum number that can be stored in a directory is slightly over 32,500, taking approximately 2 megabytes of space. I tested the system on a 8086 machine and found it a bit slow, (9000 entries is quite a few to scan). I expect that the performance would be much better on a 286 or faster machine. Greater flexibility and speed in moving around through the master list would also improve the performance of the system. The manual is written in English, has an index, and is quite good, as computer manuals go. More than half of the manual is devoted to a series of tutorials which cover nearly all features of the system. One feature lacking from the system is geographic range data for each species. This would permit the user to set up target lists for new places to visit. Perhaps future updates will include this information.

This is a very good deal for birders who have a lot of data from various parts of the world (and who have time to enter them!). The computerized world list, alone, is worth the price.—D. Scott Wood.

Resident Forest Birds in Thailand, Their Status and Conservation. By Philip D. Round. International Council for Bird Preservation, Monograph No. 2. Cambridge, U. K., 1988: 211 pp., 17 tables, 17 maps. 16 halftone photos, 4 line drawings of birds. Paper, $12.00.—This is a resume of the status and location of birds in a political entity, Thailand, the type of which is needed throughout the world. Rather than include all species, Round considers the places where wildlife is supposed to be protected and discusses the ecological conditions extant and the species being affected by the changes that each area is undergoing.

The contents of the book are arranged under seven major headings: Geography and climate of Thailand; Vegetation; Conservation measures (at present); Threats (to the birds and their environments); Regional analysis (by the six zoogeographical regions of Thailand); Species status review; and Discussion and Recommendations (for conservation). Topics under each of these headings are lucidly discussed. Among the most pertinent to me was the list of parks and wildlife refuges under "Regional Analysis", and their descriptions. I had visited

many of these areas during the past two decades and could visualize the changes in vegetation and wildlife populations. Under "Species Status Review" is found a list of the bird families in Thailand and the 93 species of birds endangered, threatened or vulnerable. An appendix of 60 pages listing the species found in Thailand makes up about one-third of the book. With all of these discussions and identifications the book is extremely valuable as a reference concerning where to go to find birds, what species are present and what conditions the observer can expect to find. We need such books for the rest of the world as aids for the serious conservationist. I.C.B.P. is to be commended for having supported this study.—H. E. McClure.

A Birdwatcher's Cookbook. By Erma J. Fisk, illus. by Louise Russell. W. W. Norton & Co., New York. 1987: 272 pp. $15.95.—A review of a *cookbook* in a scientific journal? In this case, it is easily justified because *Wilson Bulletin* readers watch birds and do field work; and we all eat. This volume serves both occupations delightfully.

If you've never encountered Jonnie Fisk's writing before—either of her best-selling amateur ornithologist-travel-adventure-philosophy books, one on surveying the birds of a remote Arizona mountain ("The Peacocks of Baboquivari," 1983) and the other on banding in Belize ("Parrots' Wood," 1985, both published by Norton) or even her pamphlet on banding ("The Bird with the Silver Bracelet," Arey's Pond Press, South Orleans, MA, 1986)—you have a treat in store. This lady is unique. I hasten to add that she is also a good friend, but I hope that does not disqualify me as a reviewer. In any case, her books reveal so much of her character that even if you don't know her when you begin page 1, you will probably finish the book counting her as a friend, or at least a kindred spirit.

The main theme of this book is how to eat well and interestingly without taking a lot of time in the kitchen, spending that time outside instead; it is also how to cook *for* people doing field work. This is no ordinary cookbook. It contains, for instance, suggestions for healthy and hearty breakfasts for a long day of birding, banding, censusing—wonderful varieties of pancakes, muffins, and biscuits that will carry you for hours in the field. It also advises on breakfasts for "birders" in too much of a hurry to sit at a table." There are many "lunches to go," containing ideas to escape the boredom of peanut butter as basic field food. An essay on why a bagel and cream cheese is so practical notes: "It fits in a pocket; it is slow chewing so it lasts a long time; you can eat it while looking through a telescope or driving without fear of dribbles on your shirt; it sticks together; if you drop it in the sand, it is easy to wipe off."

There are also hot and quick meals for when you can get home for lunch or when you come back too tired after a long day to fix a complicated meal for fellow-birding guests. Field cooking is included as well, with unusual and practical ideas. Throughout the book, there is an emphasis on good nutrition (she slips wheat germ, yogurt, and the like into all sorts of unexpected dishes) and on vegetarian foods (*good*-tasting ones).

This is a cookbook, certainly, but like all of Jonnie Fisk's books, it is highly personal; it contains short vignettes of her experiences, fellow "bird people," and thoughts on life, in amongst the recipes gathered by an interesting and creative woman during a lifetime of cooking and living. A particularly sensible defense of stay-at-home wives appears between Acorn Squash with Apple, and Pumpkin Casserole (pp. 118–119.)

She includes recipes from her home base of Cape Cod (especially rich with useful fish recipes and good things to make with cranberries), as well as many from her experiences in Florida (roast armadillo!), the American Southwest, Mexico, Central and South America, and Europe. As a diplomat's wife before she was widowed and became involved with the world of birds, Jonnie traveled and entertained a good deal. Some of her recipes from those

years—especially novel ideas for appetizers and punches—are as appropriate for a Christmas Countdown party as for a formal occasion.

Other inclusions that might not be expected in a birdwatcher's cookbook are some good recipes for bread, imaginative condiments and preserves. Her sense of humor is apparent throughout but I particularly enjoyed her advice to remove the chicken feet from soup before serving (a flavoring trick learned during Central American field work, when chickens were rare and food generally hard to come by). The reader might expect directions for sparrow pie (p. 58), comments on eating road- and window-kills after preparing them as specimens (pp. 104–5), and recipes for game, but perhaps not a tongue-in-cheek version of Elephant Stew: "Cut 1 medium-sized elephant into bite-sized pieces . . . "

"A Birdwatcher's Cookbook" is a book to be *read,* not just to look up a recipe in. The recipes are there, of course, and the main subjects are indexed, but much will be lost without a thorough reading, along with annotating the somewhat skimpy index with items especially interesting to the reader. This book is typical of the author in that it occasionally goes off on tangents: for instance, in the fish chapter Eleanor's Chowder is followed immediately by Chocolate-Chip Cookies (another recipe from Eleanor) and then Fried Grasshoppers (which Eleanor cooked when she lived in the Solomon Islands)—then back to the next fish recipe. The author's skill and approach to cooking is reflected by many of the recipes being written in a sort of short-hand, telling the reader what is in the dish but often not how much of each ingredient. A novice cook can learn much about improvisation from this breezy attitude toward hard-and-fast recipes, but advice should be sought in cases of doubt. For instance, in Black-eyed Rabbit, there are no instructions to *cook* the dried peas after soaking; inexperience could result in pretty crunchy rabbit! I noticed about 6 obvious typographical errors and suspected a few omissions, like the lack of any flour in the peanut butter cookies on p. 214. The copy of the book that I bought had "add 2 scant cups of flour" written in the author's hand in the molasses cookies recipe on the next page, and Jonnie wrote me (without knowing about this review) that 3 Tbs of shortening was inadvertently omitted from Five-Grain Bread (p. 153); despite five proofreadings, some omissions got through.

I can heartily recommend this book to all who get out to watch birds and even to those who don't. It is reasonably priced, with the royalties going to the Cornell Laboratory of Ornithology (E. Fisk, pers. comm.). It is attractively illustrated with pen-and-ink drawings. I found it thoroughly enjoyable and useful. [*Note added in proof:* I regret that publication of this review was delayed and Mrs. Fisk never saw it in print; she died peacefully in her sleep in January, 1990, at age 84. I am glad to report, however, that two more Fisk books, on natural history and Cape Cod, are in press.]—Mary H. Clench.

The Common Loon: Spirit of Northern Lakes. By Judith W. McIntyre, illus. by Anne Olson. University of Minnesota Press, Minneapolis, Minnesota. 1988:xii + 228 pp., 22 tables, 40 figures, 10 plates of color photographs, 3 appendices, 13 pp. references, 1 disc-recording of vocalizations. $25.00 cloth.—For someone who has enjoyed the lonely call of the Common Loon (*Gavia immer*) across a northern lake on a summer evening, this book will be a delight. Pleasant recollections of loon behavior and vocalizations will be recalled when reading the text and listening to the accompanying record.

This book will be appealing, as well as beneficial, to both the amateur and professional ornithologist. It is a comprehensive monograph of the natural history of the Common Loon, including chapters on loon myths and legends, courtship, nesting, territorial behavior, family behavior, social interactions, vocal communications, feeding, parasites and diseases, ecology, evolution and classification, anatomy and plumage, distribution and migratory routes, and human impact on loon populations. The author has incorporated an extensive review of the scientific literature into the text, tables, and figures, making it a valuable scientific review,

rather than just an anecdotal review. Yet the author has managed to present the findings in such a way as to explain what is known quantitatively about the loon in a format that will be enjoyable and educational reading for the amateur.

The illustrations are very well done and enhance the descriptions in the text. The recordings of Common Loon vocalizations are a positive and instructive addition. For the "loon watcher," this book will be a valuable source for understanding the behavior and calls that are observed. For the professional ornithologist, it will be a rich resource of references regarding the Common Loon, with an extensive reference section.

All of these factors take this book off the coffee table as a nice compilation of loon photographs and anecdotes, and make it a valuable and enjoyable contribution to an ornithological library. The price also will make it appealing to a variety of readers.—LEANN B. BLEM.

BIRDS AND BERRIES/A STUDY OF AN ECOLOGICAL INTERACTION. By Barbara and David Snow. T & A D Poyser Ltd., Staffordshire, England, 1988:268 pp., 44 pencil sketches by John Busby. $37.50.—The Snows continue their contribution to the field study of the coevolution of birds and fruits eaten by birds. The main basis of this book is their study of frugivorous birds in southern England from 1980 to 1985, with more than 1,600 h of timed watches at fruiting plants (43 species). As will be explained below however, the analyses of the study are of broad interest, far beyond the regional data. The book has three natural sections: the fruits, the fruit-eaters, and interpretation. In the 100 p. section on "The Fruits" individual plant species are discussed with particular attention to the seasonal pattern of avian exploitation. Let me provide an example with their text on Haws (*Crataegus* spp.), a main constituent of British hedgerows. This 4-page account reviews the distribution and abundance of haws in England and the study area. Botanical information on the haw fruits are provided (with additional information in the appendices of all fruits). The seasonal pattern of birds feeding on haws is presented with a monthly table of 3658 feeding records by eight bird species that are dispersers. Also, a very interesting histogram (Fig. 4, p. 46) shows that haw exploitation varies greatly depending on whether or not the individual plants are a defended food resource of Mistle Thrushes (*Turdus viscivorus*). The long-term defense of these plants can extend over several months, and indeed the same individual plants may be defended year after year. There is also discussion of seed- and pulp-predators. The Blue Tit (*Parus caeruleus*) are pulp-predators, taking pieces of the pulp but leaving the haw fruits in situ, while the aptly named Hawfinch (*Coccothraustes coccothraustes*) is the plant's only avian seed-predator. The account concludes with a review of "haws elsewhere," a discussion of published observations from various locations on the European continent. Most of the plant species accounts follow a format quite similar to the one described above.

In the second part of the book, the "Fruit-eaters," the many birds are discussed, again by species accounts. Remarkably, although there is a shared data as the basis of this and the first section of the book there is really little repetition in text: the plant and the bird viewpoints of the two sections turn out to be quite different. Again I will use an example to show the format. The 5 pages on the European Starling (*Sturnus vulgaris*) outlines the bird's seasonal abundance and fruit-feeding habits. A monthly table presents 4621 records of starlings feeding on fruits. Analyses show that the starling feeding success rate is often quite inferior to that of thrushes, and the behavioral and anatomical reasons for starling inefficiency in fruit feeding are considered with regard to a variety of plant species. The account ends with "starlings elsewhere," citing other European studies that include reviews of agricultural fruit-damage by starlings.

The final section of the book, "Interpretation," reviews and expands our current ecological understanding for birds/fruits interactions with discussions including studies throughout the

world by many researchers. This part of the book can be read by itself for the excellent presentations on a wide variety of topics: fruit size and seed burden, color and taste of fruits, competition for dispersal, seasonal fruit quality, seed-predators and plant defenses, limits and adaptations to a fruit diet, preferences and strategies of fruit-eaters, time/energy budgets, and coevolution (both long-term and recent) of birds and their plant foods. The Snows go far beyond their good reviews of each of these topics; they also include new ideas and novel explanations, some of which will be controversial. The study of frugivorous birds is a popular research area, with many directions, and this book serves as an important update.

Appendices include information such as the nutritive values of bird-dispersed fruits. The artistic sketches of birds and their food plants are a welcomed addition throughout the text. The book's physical quality is high; the index however could have been more complete with subject headings. One can enthusiastically recommend the book to a wide audience, from avian ecologists to the interested layman. It inspires readers to long-term, direct field observations within an observer's home district. We can extend an appreciative congratulations to the authors on a study and book well done.—Charles F. Leck.

A Guide to Bird Behavior. volume iii. By Donald W. Stokes and Lillian Q. Stokes, illus. by Bob Hines and Donald W. Stokes. Little, Brown, and Company, Boston. 1989. 397 pp., numerous line drawings. $18.95 hardcover, $10.95 paperback.—This is the third in a series of guides designed to aid birdwatchers in identifying and interpreting behaviors seen in the field. The book follows closely the format of the first two volumes (see review, *Wilson Bull.*, 96:510–511, 1984). Briefly, the book is divided into 25 sections, each devoted to a species of North American bird. Each section contains a short introduction to the species; a behavior calendar showing months when various categories of behavior can be observed; a display guide, outlining the form and context of the major visual and auditory displays; and behavior descriptions, narratives detailing major aspects of behavior such as territoriality, courtship, breeding, migration, and flocking. As was true of the first two volumes, the book is basically well done, providing a great deal of accurate information in a clear and easily retrievable fashion.

One difference between this and the previous volumes lies in the manner in which species were chosen for inclusion. As the authors explain in their introduction, the first two volumes concentrated on species that are both common and easy to observe, while for the present volume the authors chose species that, because of features such as large size, striking appearance, or unusual behavior, are especially attractive to humans, even though many of these species turn out to be rare or difficult to observe. Thus readers may have more difficulty in actually seeing many of the behaviors described in this volume, but on the other hand most will probably agree that those behaviors one does observe are of special interest.

The information presented has again been garnered from original scientific papers, which are listed in the back of the book but are not cited in the text. The authors for the most part have done a good job in locating the appropriate literature, though I did notice a few omissions; for example, D. W. Mock's work on sibling aggression in Great Blue Herons (*Ardea herodias*) seems to have been overlooked, as has B. Heinrich's recent work on the social behavior of Common Ravens (*Corvus corax*). Another problem is the confusion the authors occasionally exhibit about certain ethological concepts. For example, they do not seem to have a good grasp on the definitions of the various types of mating systems, and they stretch the definition of territoriality to a dubious degree, as when they categorize defense against potential nest predators under this term. Moreover, they also seem confused at times about how natural selection works in the evolution of behavior. The most glaring

example of this problem is the puzzlement they repeatedly express about the function of brood parasitism, a behavior whose probable fitness benefit to individual practitioners seems especially obvious.

Despite these problems, the book is an excellent resource, providing an introduction to the behavior of the target species that should be useful to professional and amateur ornithologists alike.—William A. Searcy.

Birds in Kansas. Vol. 1. By Max C. Thompson and Charles Ely. Univ. Kansas, Mus. Natural History, Lawrence, Kansas. Public Educ. Ser., No. 11 (J. T. Collins, ed.), distributed by The Univ. Press of Kansas, Lawrence, Kansas. 1989:xv + 404 pp., 179 black-and-white photos, 222 distribution maps. $25.00 (cloth), $14.95 (paper).—As should be expected from the state's central position among the 48 contiguous states, the birds in Kansas show both eastern and western as well as northern and southern affinities, resulting in a state total of 424 species. The authors identify the Zebulon Pike expedition in 1806 for the addition of the first species to the recognized list for what is now Kansas. The history of ornithology in Kansas is the history of western expansion and the naturalists who accompanied the army during this invasion—Say, Abert, Baird, Cassin, Couch, Hammond, and Coues, to name a few. The most recent synopsis of Kansas birds was R. F. Johnston's 1965 "Directory" (also published by The Museum of Natural History at the Univ. of Kansas) that listed 383 species. Several of the professional ornithologists in the state who have enriched the state list during the intervening quarter century are identified by Thompson and Ely, but unfortunately none of the highly proficient amateur ornithologists are recognized.

The authors' purpose is not to provide a "thorough technical work, but rather . . . for the enjoyment and use of both the amateur birdwatcher and the professional ornithologist." The bulk of the book is devoted to the accounts of 222 non-passerine species (including the extinct Passenger Pigeon [*Ectopistes migratories*] and Carolina Parakeet [*Conuropsis carolinensis*]. Volume 2 will cover the passerines. For every species a statement of occurrence and abundance is provided. For 162 species this status report is expanded to included paragraphs on "periods of occurrence" and "habits and habitat." For 105 species there is a section on "breeding," included for some species that do not breed in the state (e.g., Purple Gallinule [*Porphyrula martinica*], Piping Plover [*Charadrius melodus*], and Willet [*Catoptrophorus semipalmatus*]) and excluded for one species that does breed in the state (Whip-poor-will [*Caprimulgus vociferus*]). Field marks are described for 45% of the species, but there appears to be no pattern to the inclusion of this section. The American Swallow-tailed Kite (*Elanoides forficatus*), described as "unmistakable" and the Black-necked Stilt (*Himantopus mexicanus*), "one of the most easily identified shorebirds" receive space under this heading, while no species in the genus *Accipiter* does. For almost three-quarters of the species, there is a description of "food," a section that could have been omitted without any significant loss.

The major contribution of this book, in addition to providing an authorative list of the species in the state, is the distributional data. Every species has a state map with the counties of record indicated, even if there is only one dot. This presentation, of course, will be a major stimulus for further distributional work as we all go out to fill in the blanks (I've already started my file). It would have been also helpful if a figure providing a graphic presentation of phenology and relative frequency of the species could have been included, but perhaps the authors felt that a similar figure in the recent guide to bird-finding in the region (Zimmerman and Patti 1988, Univ. Press of Kansas) was sufficient.

There are black-and-white photographs with 187 of the species' accounts provided by 23 bird photographers, the work of David Rintoul, Galen Pittman, Bob Gress, Marvin Schwill-

ing, Frank Shipley, Mike Blair, and Jean and Ed Schulenberg being well represented. Some abundant species are not pictured (e.g., Common Merganser [*Mergus merganser*]), some rare species for which good Kansas photos exist are not included (e.g., Thayer's Gull [*Larus thayeri*]), and there are some errors in the captions that will cause confusion (e.g., Black-bellied Plover [*Pluvialis squatarola*] in "winter" plumage, the "Baird's" Sandpiper [*Calidris bairdii*], and the "adult White-faced" Ibis [*Plegadis chihi*]).

My only disappointment is the paucity of literature citations. Even though this is not a strictly scientific work, it would have been more satisfying if at least all the published records that substantiate species' occurrences could have been included. A comprehensive bibliography for Kansas birds has not been available since Johnston's work. Hopefully this will be rectified by the rapid publication of the more technical treatment of Kansas birds by the authors.

The authors dedicated this volume to colleagues "who waited so patiently", and I believe that it was worth the wait. We anticipate the publication of volume 2 with positive expectations.—John L. Zimmerman.

Audubon Wildlife Report 1989/1990. By William J. Chandler (ed.) Academic Press, New York. 1989:xix + 585 pp., many black-and-white photos, maps and graphs. $39.95.—This is the fifth volume in a series of summaries which emphasize the wildlife management activities of various agencies of the Federal Government. Earlier volumes were reviewed in *The Wilson Bulletin* 100:707–708(1988) and 101:522(1989) and the current volume follows the format outlined in those reviews.

"The Featured Agency" in this volume is The U.S. Army Corps of Engineers, and this is the only Federal agency discussed in this volume. Part Two reports on eight "Conservation Challenges." These include two articles of great interest to ornithologists: "Conserving Nongame Migratory Birds: A Strategy for Monitoring and Research" by Judith Gradwohl and Russell Greenberg, and "Global Warming, Climate Disruption, and Biological Diversity" by R. T. Lester and J. P. Myers. The others discuss Western Water and Wildlife; The Pacific Northwest's Ancient Forest; Recent Court Decisions affecting Wildlife; Conserving Southeast Coastal Wetlands; Discarded Catch in U.S. Commercial Marine Fisheries and Restoring Ravaged Range.

Part Three (Case Histories) discusses eight species (two mammals, four birds, one fish and one insect (monarch butterfly) that are either endangered or are involved in some conservation problem. The bird species are the Hyacinth Macaw (*Anodorhynchus hyacinthinus*), the Marbled Murrelet (*Brachyrhamphus marmoratus*), the Roseate Tern (*Sterna dougallii*), and the Golden Eagle (*Aquila chrysaetos*). The accounts include an outline some of the natural history of the species, an Historical Perspective and sections on Current Trends, Management, Prognosis, and Recommendations.

A series of Appendices provides a set of directories for the various agencies as well as other useful information including a listing of the Federal Endangered and Threatened Species.

This series has produced some very informative volumes, but one wonders about the selection of this method of getting the information to the public. The volumes are too expensive for the individual, and most institutional libraries may not want to spend their dwindling funds on another series of glossy books, when a more conservative and cheaper publication scheme might suffice.—George A. Hall.

American Warblers. An Ecological and Behavioral Perspective. By Douglass H. Morse. Harvard University Press, Cambridge, Massachusetts. 1989: xii + 406pp., 57 black-

and-white figs. ISBN 0-674-03035-4. $30.—An arguable case can be made that more bird students would select the wood warblers (Parulinae) as their favorite group of birds than any other group. The author of this book admits that warbler watching played a large part in starting him on his biological career and no doubt many other ornithologists (including this reviewer) would make the same admission. Over the years there have been numerous books on warblers, some accounts of life histories, some elaborate picture books, and some written for the popular market. Here at hand is a book which, as the subtitle indicates, goes beyond anecdotal life history information, and is the first real attempt to synthesize a modern treatment of the biology of this diverse group.

In the 1960s and '70s ornithologists knew Doug Morse as an innovative student of warbler behavior and ecology in the spruce forest of Maine. More recently we heard rumors that, deserting ornithology, he had turned his attention to animals other than birds, but with this book we welcome him back into the fold.

A more representative title might have been "Some American warblers" because the coverage is highly variable. As we might expect from the author's principal research interests, three or four of the spruce-forest warblers of the northeast receive much coverage. Other species that receive full coverage are the Prairie Warbler (*Dendroica discolor*), based on Nolan's exemplary monograph, two threatened species, The Kirtland's (*D. kirtlandii*) and the Golden-cheeked (*D. chrysoparia*), which have been monographed, as well as the Golden-winged (*Vermivora chrysoptera*)—Blue-winged (*V. pinus*) complex. The warblers of the eastern deciduous forest come off with much less discussion, while the western warblers are skimpily treated and one—*Vermivora virginiae*—is omitted entirely. This unevenness cannot be blamed on the author, but is an accurate reflection of the amount of the study that has been devoted to the various species. The 37 pages of bibliography attest to the thoroughness of the author's coverage of the work that has been done on these species.

Besides reporting the known facts, Morse does not hesitate to share with us his insights into the meaning of it all. Each chapter is sprinkled with fascinating and provocative ideas and suggestions, but my only disappointment with the book was that there weren't even more of these.

The list of chapter titles illustrate the wide gamut of topics taken up: Distribution and Evolutionary History, The Breeding Season, Foraging, Habitat Selection and Use, Territorial Behavior and Other Aspects of Resource Exploitation, Predators and Parasites, Display, Plumages, Migration, The Wintering Season, Rare Species, Population Limitation and Species Diversity, Hybrids, Tropical Warblers, Ecological Equivalents, and Opportunities for Further Research.

The book begins with a summary of the several groups of warblers and their distribution. Morse postulates that warblers as a group originated in the American tropics but that most of the speciation occurred in the Pliocene in the southern Appalachians, with the final divergence of some of the superspecies complexes in the Pleistocene. This view seems more reasonable than Mengel's (1964) suggestion that Pleistocene glaciation was responsible for the speciation.

The chapter titled "Population Limitation and Species Diversity" is perhaps the most thought-provoking chapter in the book. Morse attempts, very sucessfully, to come to grips with the question as to how so many closely related species can occupy a limited habitat. This topic is also treated in the habitat selection chapter. This chapter also gives a thoughtful treatment of the current debate about limitation of numbers by factors on the breeding grounds as opposed to the limitation by factors on the wintering grounds, with limitation by migration events thrown in. Morse concludes that all of these factors are important.

There is an interesting suggestion that the spruce budworm control measures have stabilized the populations of the so-called "budworm specialists" by keeping the insect population at low to medium epidemic proportions. Without the control measures there would

have been such extensive tree-kill that large areas would not support budworms, and hence warblers for many years.

The chapter on foraging concentrates on the breeding season and, as expected, dwells extensively on Morse's work on the spruce-woods warblers. The interesting suggestion is made that during wet weather, or in damp environments, the birds will prefer red spruce forests to white spruce because of the difference in needle arrangement.

The chapter on display is concerned mostly with vocalizations. I found the section on Song and Environment, with its discussion of the attenuation of sound intensity with distance in the forested habitat especially interesting. The chapter on plumages compliments this with a stimulating discussion of plumage patterns and their origins and uses. Especially interesting is the discussion of the relation between certain plumage features and the amount of light the birds experience in foraging as well as on their singing perches.

The chapter on migration discusses the routes used and dwells heavily on the ecology of the habitat changes the species undergoes as it moves between breeding and wintering grounds. It is emphasized that little work has been done on the factors involved in habitat selection during migration. The chapter on the wintering season seems to be an essentially complete summary of the as yet not too extensive information on wintering ranges and behaviors.

A chapter on hybrids discusses the *Vermivora* complex thoroughly and other hybrid combinations, including Sutton's Warbler (*D. potomac*) are mentioned. Morse is favorably inclined to the suggestion of Parkes that intergeneric hybrids should be more common than intrageneric ones.

In addition to the Kirtland's and Golden-cheeked warblers, the chapter on rare species treats the Bachman's (*V. bachmanii*) and Swainson's (*Limnothlypsis swainsonii*) warblers as well as some formerly rare ones that have increased. The Colima Warbler (*V. crissalis*) is barely mentioned. The very interesting suggestion is raised that the current rarity of Bachman's Warbler may have something to do with its relationship with the Northern Parula (*Parula americana*).

The chapter on tropical warblers is brief, reflecting the dearth of work on these species, but the differences resulting from the sedentary vs migratory life styles are pointed out. The penultimate chapter draws some interesting contrasts between the New World Parulines and the Old World Sylviids.

In the final chapter Morse lists some opportunities for further research and these are all thoughtful ideas. However, as I read through the book I was constantly being reminded of things we apparently do not know about these birds. Why, for example, does the male American Redstart (*Setophaga ruticilla*), and no other warbler, require two years to acquire its fully adult plumage? Why is the sexual dichromatism of the Black-throated Blue Warbler (*D. caerulescens*) so much more marked than in other species? The whole book can be a fruitful source of research ideas. The book is readable and there are a minimum number of typos. Most readers will rejoice in the absence of the highly mathematical treatment so common in modern ecological papers, but the science is good for all of that lack. This important book should be read by all eco-ethologists (or etho-ecologists) as well as by paruliphiles.—GEORGE A. HALL.

BRIEFLY NOTED

The following publications are available (Free of Charge) from the Publications Unit, U.S. Fish and Wildlife Service, 18th and C Streets, NW, Room 130 Arlington Square Building, Washington D.C., 20240.

North American Breeding Bird Survey, Annual Summary 1988. By Sam Droege and John R. Sauer. U.S. Fish and Wildlife Service Biological Report 89(13), 1989:16 pp.—G.A.H.

Procedures for the Analysis of Band-Recovery Data and User Instructions for Program Mult. By Michael J. Conroy, James E. Hines, and Byron K. Williams. U.S. Fish and Wildlife Service Resource Publication 175. 1989:iii + 61 pp.—G.A.H.

Demographic Characteristics of a Maine Woodcock Population and Effects of Habitat Management. By Thomas J. Dwyer, Greg F. Sepik, Eric L. Derleth, and Daniel G. McAuley. U.S. Fish and Wildlife Service, Fish and Wildlife Research 4. 1988:iii + 29 pp.—G.A.H.

Migration of Radio-marked Whooping Cranes from the Aransas-Wood Buffalo Population: Patterns of Habitat Use, Behavior, and Survival. By Marshall A. Howe. U.S. Fish and Wildlife Service, Fish and Wildlife Technical Report 21. 1989:iii + 33 pp.—G.A.H.

A Computer Program for Sample Size Computations for Banding Studies. By Kenneth R. Wilson, James D. Nichols, and James E. Hines. U.S. Fish and Wildlife Service, Fish and Wildlife Technical Report 23. 1989:19 pp.—G.A.H.

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The superspecies *Stachyris* [*striata*] superimposed on a map of the Philippines with (from top to bottom) *S. striata* from Luzon, *S. latistriata* sp. nov. from Panay, *S. nigrorum* from Negros, and *S. hypogrammica* from Palawan. Painting by John A. Ruthven.

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A NEW SPECIES OF *STACHYRIS* BABBLER (AVES: TIMALIIDAE) FROM THE ISLAND OF PANAY, PHILIPPINES

PEDRO C. GONZALES[1] AND ROBERT S. KENNEDY[2]

ABSTRACT.—*Stachyris latistriata,* sp. nov., is described. It is known only from the mountains of Panay in the central Philippines, where it occurs commonly in montane forests above 1000 m. Notes on its behavior, breeding condition, nest and vocalizations are presented. It is a member of the superspecies *Stachyris* [*striata*] which contains three other Philippine endemics. *Received 7 March 1990, accepted 6 April 1990.*

The ornithology of the island of Panay in the central Philippines perhaps is the least known of the main islands of the Archipelago. Although Sonnerat (1776) first visited Antique, Panay in 1771, more than a century passed before other collections were obtained from the island by the Steere Expeditions in December 1874 (Sharpe 1876, 1877) and January 1888 (Steere 1890) and by the Menage Expedition (Bourns and Worcester 1894) in November 1890. A few additional collections were made in the earlier part of this century by Anderson between 1901 and 1912, by W. Cameron Forbes in March 1913 and again in August 1921, by McGregor (1921) in 1918, and by Manuel in 1933. For the most part these parties visited lowland areas, leaving the higher elevations of the rugged mountains bordering the west coast of the island virtually unexplored.

Since so little work had been done on Panay and because the original lowland forests on the eastern side of the island have for the most part been destroyed, recent collectors and naturalists visiting the Philippines have ignored it.

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Fortunately, in February and March 1987 a team of collectors led by Rogelio Sison from the National Museum of the Philippines (NMP) set out to determine the status of the endangered deer *Cervus alfredi* in the remaining forests of Mt. Baloy, which lies at the junction of the provinces of Antique, Capiz, and Iloilo in west central Panay. During their study, they also collected 77 bird specimens. One of the specimens mist-netted in montane forest was an unidentified bird that clearly belongs in the babbler genus *Stachyris*. We compared the specimen to other members of the genus, particularly the Luzon Striped Babbler (*Stachyris striata*) from Luzon and the Negros Striped-Babbler (*S. nigrorum*) from Negros, and concluded that it represented a new species. However, with only one specimen in hand, we decided that a larger series was needed before we could describe the species. This gave rise to the National Museum of the Philippines/Cincinnati Museum of Natural History (NMP/CMNH) Expedition that departed for Mt. Baloy on 25 September 1989 and stayed on until 19 October 1989. On this expedition, we obtained a series of 35 specimens (skins with trunk skeletons—7 ♂, 6 ♀; skins alone—11 ♂, 7 ♀; fluid-preserved specimens—1 adult, 2 nestlings; whole skeletons—1 ♀; frozen tissue from 6 ♂, 4 ♀) of the new taxon, plus additional birds, mammals, reptiles and amphibians and other terrestrial and freshwater animals. This rather large series of new material added support to our earlier conclusion and here we describe and name the new species as:

Stachyris latistriata, sp. nov.

PANAY STRIPED-BABBLER

HOLOTYPE.—NMP 16663, female (with skull 75% ossified, ovary measuring 6 × 4 mm, and the presence of a brood patch), collected 7 October 1989 at an elevation of 1530 m, 11°8′N, 122°14′E, 1.1 km south southwest of the peak of Mt. Baloy, Barangay San Agustin, Municipality of Valderrama, Antique Province, Panay, Philippines by the National Museum of the Philippines/Cincinnati Museum of Natural History Expedition, field number 2048.

DESCRIPTION OF HOLOTYPE.—Lores pale Cream Color 54 (capitalized color names and numbers are from Smithe 1975, 1981) grading into cream white in lower superciliary, auricular, and malar region; band of black on the forehead extending into the forecrown, upper superciliary and looping behind and below the auriculars; eye-ring cream white; crown and nape Greenish Olive 49 a shade darker than the back, which becomes lighter toward the rump; upper tail coverts rusty olive; tail dark Greenish Olive with a tinge of rust; edges of the rectrices have the same color as back; primaries Sepia 119 with pale yellow outer edges; secondaries dark Olive Green 48 with outer edges same color as the back and inner edges pale yellow; spot distal to bend of wing light Sulphur-Yellow 57; chin and upper throat cream white; lower throat light Sulphur Yellow becoming Buff-Yellow 53 on breast and belly; flanks including shank features Greenish Olive; broad black streaks beginning on throat, most prominent on breast, fading to dark Olive Green on belly and under tail coverts. Soft part colors of the living holotype 1 h after capture as described by artist John Ruthven, "Eye bright rust, outer edge lighter grading to bright rust toward pupil; eye-ring pale horn;

FIG. 1. Side view of the holotype of *Stachyris latistriata* photographed less than 30 min after it was captured on Mt. Baloy.

bill with upper mandible dark horn, deeper at base and pale horn at cutting edge; lower mandible dark horn at the tip grading to light horn toward the cutting edge; gape pale horn with greenish overtone grading posteriorly to dull ochre then pale flesh; tongue pale horn at tip grading posteriorly to pinkish white; under-tongue pale flesh; legs and feet bluish olive; toe pads medium chrome yellow fading to lighter on edges; nails horn, darker on ridge." (See Figs. 1 and 2).

PARATYPES.—NMP 16358, collected 6 March 1987 from Mt. Baloy, Iloilo Province, Panay at an elevation of 3300 ft (ca 1000 m); and NMP 16664–16677 and CMNH 34211–34226, all collected from 7 to 13 October 1989 at elevations from 1530 to 1540 m at the type locality.

PARATYPIC VARIATION.—Overall colors vary from slightly darker to slightly paler than the holotype. There is variation in the intensity of color of the black streaks, which normally are confined to the breast but may occasionally (especially in males NMP 16358, 11673 and CMNH 34211, and female CMNH 34226) extend onto the belly. The black patch on the forehead and forecrown also varies in some specimens (particularly males NMP 16664, 16677, and female NMP 16675) with black feathers extending onto the crown just posterior to the eyes. Plumage variations seem to be individual and do not reflect the sex or age of the specimens in the series. The sexes are different in size, with males significantly (two sample t-test, $P < 0.05$) larger than females in weight, length of culmen, bill width and tarsus length, and highly significant ($P < 0.01$) in wing chord. Differences in tail length and distance from the bill tip to the nostril were not significant.

MEASUREMENTS.—Holotype: wing chord 70.0; tail 53.5; tarsus 24.2; culmen 20.9; bill width at feather line 5.8; bill-tip to anterior edge of nostril 11.6. Males: wing chord (19)

FIG. 2. Frontal view of the holotype of *Stachyris latistriata* photographed at the same time as Fig. 1.

71.0 ± 1.56, range 68.6–75.2; tail (18) 55.4 ± 1.50, range 53.1–58.4; tarsus (19) 24.3 ± 0.62, range 23.1–25.5; culmen (19) 21.2 ± 0.51, range 20.1–22.0; bill width at feather line (19) 6.0 ± 0.32, range 5.4–6.7; bill tip to anterior edge of nostril (19) 11.4 ± 0.52, range 10.3–12.1. Females: wing chord (13) 69.2 ± 1.35, range 67.3–72.5; tail (12) 54.8 ± 1.61, range 53.3–58.7; tarsus (12) 23.8 ± 0.51, range 22.7–24.6; culmen (13) 20.9 ± 0.42, range 20.3–21.6; bill width at feather line (13) 5.7 ± 0.34, range 5.3–6.4; bill tip to anterior edge of nostril (13) 11.4 ± 0.31, range 11.0–11.9. Combined measurements of males and females are presented in Table 1.

WEIGHTS.—Holotype 30.5 g; males (15) 29.3 ± 1.92, range 25.5–31.5; females (12) 27.2 ± 2.13, range 24.0–30.5.

DIAGNOSIS.—*S. latistriata* clearly falls in the superspecies of *Stachyris* [*striata*], which consists of *S. striata* from Luzon, *S. nigrorum* from Negros, and *S. hypogrammica* from Palawan (see Frontispiece). Phenotypically it appears more closely related to *S. nigrorum* of nearby Negros, less so to *S. striata,* and farthest from *S. hypogrammica,* which has the black streaks on the breast and belly characteristic of the superspecies but lacks the black band on the forehead. Also, *S. hypogrammica* differs by having the forehead and crown Cinnamon 123A, the back and rump Yellowish Olive Green 50, and the breast and belly bright greenish yellow. In Tables 1 and 2 we have summarized the salient features and measurements that distinguish *S. latistriata* from its closest congeners, *S. nigrorum* and *S. striata. S. latistriata* is clearly the largest of the three species, with highly significant differences (Mann-Whitney *U* Test, $P < 0.01$) between it and the other two in all measurements taken.

ETYMOLOGY.—Named for its characteristic broad black streaks on the breast and belly that are more pronounced than in any of its congeners.

TABLE 1

COMPARISON OF THE SALIENT CHARACTERISTICS THAT DISTINGUISH *STACHYRIS LATISTRIATA* FROM *STACHYRIS NIGRORUM* AND *STACHYRIS STRIATA*

S. latistriata	*S. nigrorum*	*S. striata*
Black band on forehead—broader and more developed	Narrower, less developed	Nearly absent
Black band around auriculars—poorly developed	More developed	Absent
Crown, hind neck and mantle—Greenish Olive 49[a]	Citrine 51	Citrine washed with Clay Color 26
Tail—Greenish Olive	Brussels Brown 121B	Mikado Brown 121C
Wings—Sepia 119 with pale yellow edges	Pale Sepia with olive yellow edges	Paler Sepia with paler yellow edges
Inner edge of secondaries—light yellow	Buffy	Pale buffy
Chin—cream white	Pale yellow	Pale yellow
Throat—cream white with black streaks	Pale yellow without streaks	Pale yellow without streaks
Breast—light Sulphur Yellow 57 becoming Buff Yellow 53 with broad black streaks	Paler with narrow black streaks	Paler with black streaks not as broad
Flanks—Greenish Olive	Pale brownish olive	Paler brownish olive
Shank feathers—Greenish Olive	Light brownish olive	Light brownish olive
Legs and feet—bluish olive	Tannish horn	Tannish horn

[a] Capitalized color names and numbers are from Smithe (1975, 1981).

SPECIMENS EXAMINED.—*Stachyris latistriata*: 9 ♂, 7 ♀ (NMP), 10 ♂, 6 ♀ (CMNH). *S. nigrorum*: 6 ♂, 11 ♀ (FMNH), 1 ♂ (USNM). *S. striata*: 2 ♂ (DMNH), 4 ♂, 2 ♀ (FMNH).

DISCUSSION

Habits and behavior.—The Panay Striped-Babbler was the most common bird in the high elevation forests of Mt. Baloy (Fig. 3) and adjacent peaks. We observed it from approximately 1400 m to the peak of Mt. Baloy at 1900 m; however, the specimen obtained in 1987 was netted at about 1000 m. This altitudinal range closely parallels the presence of mosses in the trees, with moss becoming conspicuous at 1400 m and increasing in presence to true mossy forest (Fig. 4) from 1750 m to the peak. We suspect that the species occupies this habitat throughout the high elevation forests of Panay (Fig. 5). If this is true, its total range spans 96 km with an area less than 738 km^2, the extent of the remaining closed and open canopy forests on Panay (Swedish Space Corp. 1988).

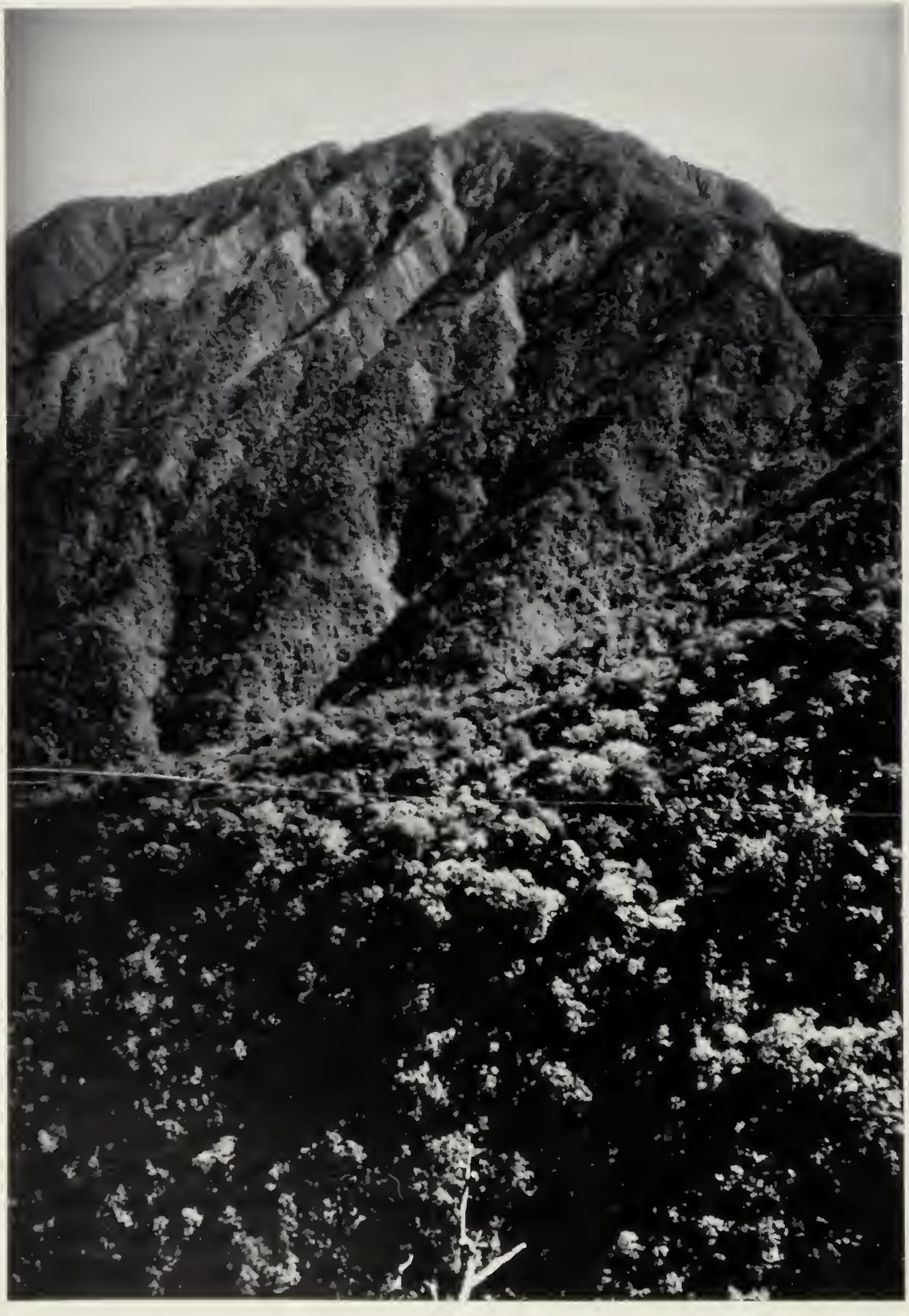

FIG. 3. View of the peak and western slope of Mt. Baloy. The holotype was obtained on the flat ridge below and to the right of the peak.

TABLE 2

MEASUREMENTS OF *STACHYRIS LATISTRIATA*, *STACHYRIS NIGRORUM* AND *STACHYRIS STRIATA*[a]

Measurements (mm)	*S. latistriata* N Mean (SD) Range	*S. nigrorum* N Mean (SD) Range	*S. striata* N Mean (SD) Range
Wing chord	32 70.3 (1.7) 67.3–75.2	18 68.9 (1.3) 66.3–71.7	7 60.2 (1.7) 58.3–63.2
Tail	30 55.2 (1.5) 53.1–58.7	18 52.0 (1.3) 50.3–54.9	7 51.3 (2.3) 48.9–55.3
Tarsus	31 24.1 (0.6) 22.7–25.5	18 23.5 (0.7) 22.0–24.7	8 17.8 (0.7) 16.8–18.6
Culmen	32 20.9 (1.6) 20.1–22.0	18 18.0 (0.9) 15.7–19.6	8 16.2 (0.8) 15.4–18.0
Bill width at feather line	32 5.8 (0.4) 5.3–6.7	18 5.4 (0.2) 5.0–5.8	8 5.2 (0.2) 5.0–5.6
Bill tip to anterior edge of nostril	32 11.4 (0.4) 10.3–12.1	18 10.1 (0.4) 9.1–10.7	8 9.4 (0.4) 9.0–10.2

[a] Highly significant differences (Mann-Whitney *U* Test, $P < 0.01$) exist between *S. latistriata* and *S. nigrorum*, and between *S. latistriata* and *S. striata* for all measurements presented.

We encountered *S. latistriata* singly or in pairs, usually in the middle and upper parts of the canopy from 3 to 12 m from the ground. They apparently do frequent lower vegetation as all 34 specimens (excluding nestlings) were captured in mist nets with the highest trammel usually set about 2.5 m from the forest floor. In at least one case we caught three birds about a meter apart in the middle of a net (1.5 m from the ground), suggesting that they occasionally travel in small groups. We did not observe them participating in mixed species flocks.

We detected these elusive birds in the forest more often by their call notes and song (described below and see Fig. 8) than by sightings. They do respond to artificial alarm and distress calls (known in bird-watching circles as "pishing" and "squeaking") made by an observer but they usually do not stay in view for more than a few seconds. Their posture while perched varies from an upright flycatcher-like stance similar to the posture of the holotype in Fig. 1 to having the head dipped below, or slightly above the level body as in the Frontispiece. Often the head is recoiled giving a "no neck" appearance. The white lores and face with dark line through the eye and the bold black streaks on the breast are this species' best field marks.

FIG. 4. Mossy forest at 1880 m on Mt. Baloy, typical habitat of *Stachyris latistriata.*

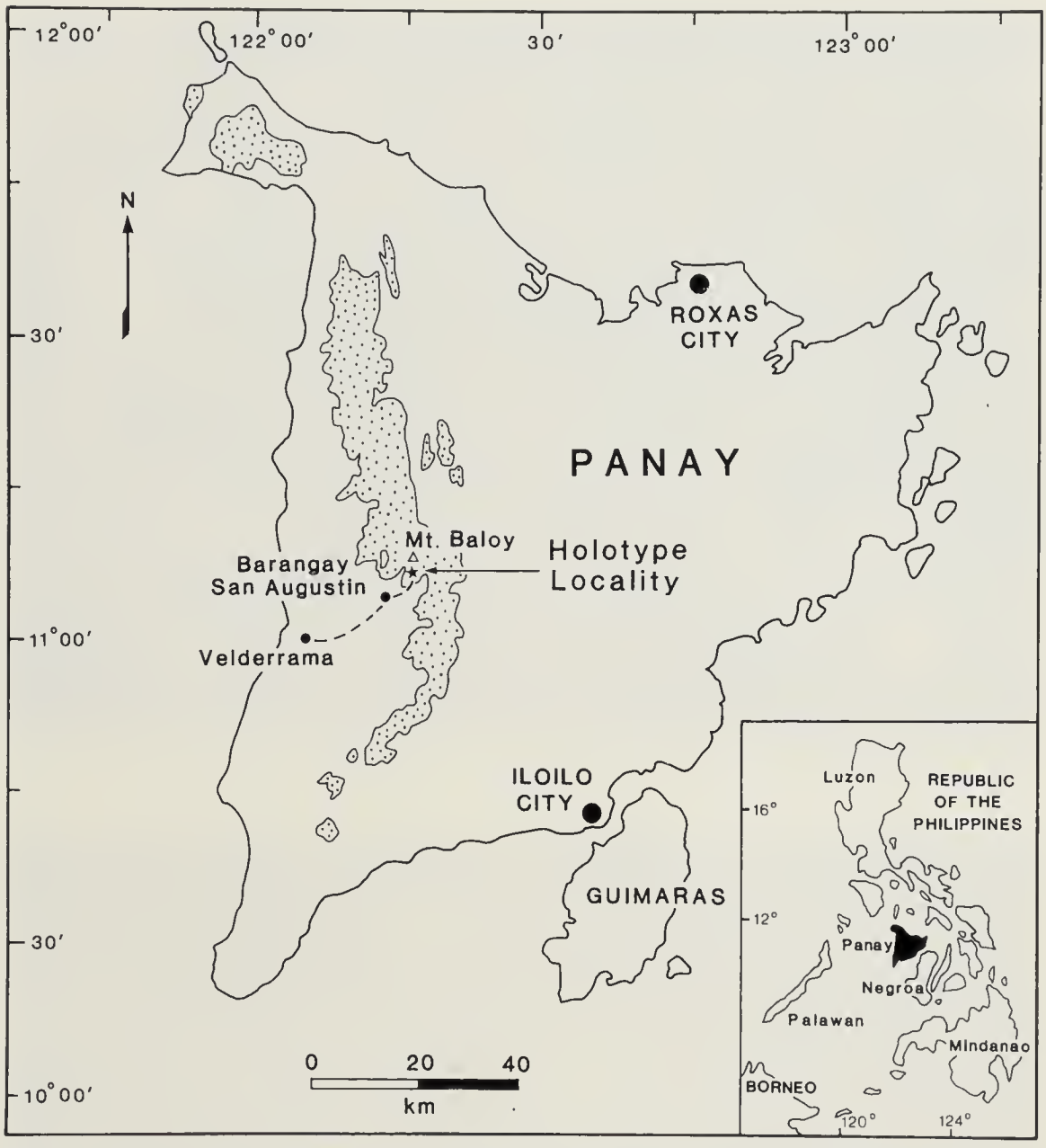

FIG. 5. Map of Panay, Philippines showing the holotype locality (star), Mt. Baloy (triangle), the route to Mt. Baloy (dashed line) and the distribution of the remaining closed and open canopy forest (stippled area) on the island.

Breeding.—Of the specimens whose gonads we measured, 8 of 14 ♀ and 13 of 16 ♂ had enlarged gonads (ovary measuring 6 × 4 to 10 × 4.5 mm; and left testis measuring from 3 × 2 to 6 × 4 mm). Enlarged oviducts were observed in 2 ♀ and a brood patch was noted in the holotype. Only 1 ♀ and 3 ♂ obtained had small gonads, and skull ossification equal to or less than 50%. We believe these were recently fledged young.

On 14 October 1989 Mila Ebreo of our field team found a nest of the Panay Striped-Babbler. The cupped nest (Fig. 6) was suspended among

FIG. 6. Nest of the Panay Striped-Babbler found at 1710 m on Mt. Baloy.

FIG. 7. Close-up of nestling Panay Striped-Babblers.

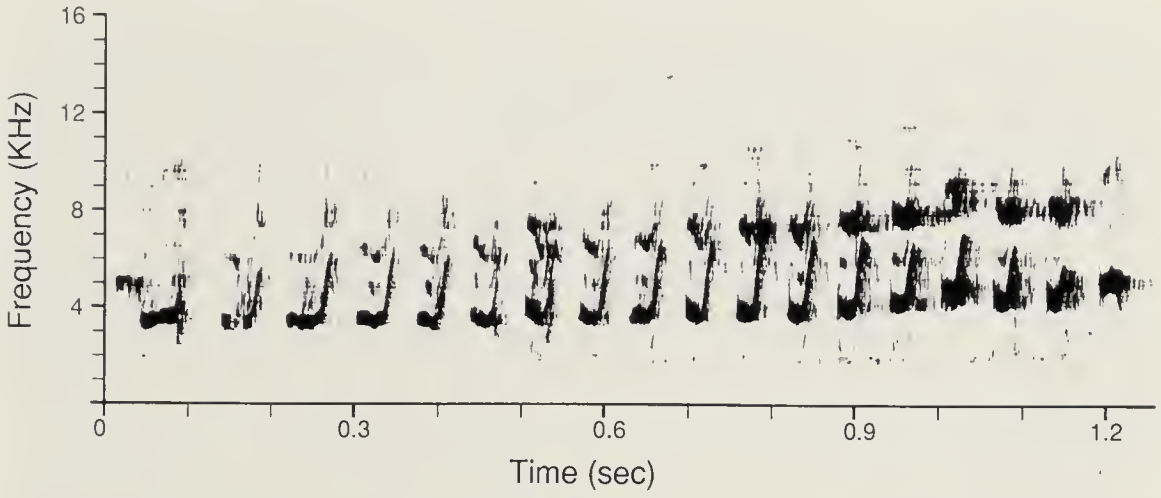

FIG. 8. Sonagram (wide band, 160–16000 Hz) of one of the trills in the song of the Panay Striped-Babbler. Recorded by R. S. Kennedy (LNS 46824) at 1690 m on Mt. Baloy.

5 small branches in the center of the crown (diameter ca 50 cm) of a small tree (*Ficus* sp., Family Moraceae) protruding from the forest canopy on a southern exposed slope. It was ca 5 m from the ground in virgin mossy forest at ca 1710 m. To identify what species the nest belonged to, Kennedy hid in the forest about 15 m away waiting for a parent to arrive. After 10 min, one *Stachyris latistriata* landed on the edge of the nest with a small round white object in its bill. Kennedy could not identify the object but believed it was a seed or small fruit. The team collected the nest and two recently hatched young (Fig. 7) shortly after the nest was identified. It had the following dimensions: overall height—70 mm, outside diameter—90 mm, inside bowl diameter—66 mm, inside depth—45 mm, and was composed of live and dead mosses loosely woven together. The nest bowl was lined with black hair-like roots from epiphytic ferns and larger tan stems from an unidentified orchid.

From gonad size, presence of fledged young in our series and the nest we found, we know the Panay Striped-Babbler was breeding in October. However, we suspect the nesting season was nearly over as testes in males were not greatly enlarged and the largest ova noted in females measured only 1.5 mm in diameter.

Food.—The stomach of NMP 16665 contained the remains of several insects including at least one coleopteran and one cicada (Family Cicadidae). A scat from the holotype contained spherical objects that appeared to be seeds.

Vocalizations.—The song consists of a series of slightly ascending trills sung from perches within the canopy of the forest. One trill (Fig. 8) lasted 1.2 sec. In the first of two recordings made, a solitary bird sang 11 (of a

longer series) trills over 39.6 sec with an average interval between trills of 3.60 sec ± 1.33 sec (range 2.46–7.41 sec). In a second recording, a bird accompanied by a second individual sang 17 trills over 2 min 23.21 sec with an average interval between trills of 8.42 sec ± 7.42 sec (range 3.03–28.32 sec). Interspersed among the long intervals between trills were call notes "tsik" and an occasional chatter-like call.

Molt.—All adult specimens in the series collected in October had one or more rectrices missing or partially grown in. Wing molt was taking place in October as well. We particularly noted wing molt in CMNH 34211, with primary 4 growing in, and in CMNH 34229 with primaries 1 and 6 appearing.

Remarks.—Like *S. nigrorum* and *S. hypogrammica, S. latistriata* is a bird of high elevation (above 1000 m) forests, while *S. striata* is a bird of low and middle elevation forests. *S. latistriata* and *S. striata* often forage singly or in pairs in the middle and upper levels of the forest (Kennedy pers. obs.), while *S. hypogrammica* forage in pairs and often in small groups of 5 or so birds at all levels of the forests (Gonzales pers. obs.). There are no published records of the foraging behavior of *S. nigrorum.* The three members of the superspecies we have seen are all noisy, active birds.

ACKNOWLEDGMENTS

We are indebted to R. Sison, who obtained the first specimen of *Stachyris latistriata,* and R. Cox, who accompanied Sison and provided the impetus for the first trip to Panay. Their pioneering work in 1987 paved the way for our recent expedition. The untiring efforts of our field colleagues D. Burt, J. Cabalquinto, E. Cañada, P. Comintan, M. Ebreo, R. Fernandez, J. Ferner, J. Lasugas, M. Manuel, L. Moores, J. Ruthven, E. Sagcal, V. Samarita, and R. Sison, and of our numerous assistants in Valderrama, are greatly appreciated. We thank the curators and staff of the Delaware Museum of Natural History (DMNH), Field Museum of Natural History (FMNH), and National Museum of Natural History (USNM) for lending specimens and/or for permission to study specimens in their care, and the Library of Natural Sounds (LNS) of the Cornell Laboratory of Ornithology for the loan of recording equipment and for preparing the sonogram. We are particularly grateful to J. Ruthven for painting the Frontispiece, L. Messick for preparing the text figures, D. Evered for assistance with statistics, C. Ross and D. Willard for assistance at their museums, D. Mindell for providing a liquid nitrogen tank, and A. Buck and K. C. Parkes for reviewing the manuscript. Our expedition was made possible through the generosity of Mrs. E. Farny, Mr. and Mrs. J. Herron, Mr. and Mrs. G. Perbix, J. Ruthven, and Mrs. G. Strietmann, and by support from Thomas More College and Outdoor Adventures. Finally, Kennedy and the CMNH team thank Mary and Michael Stephen for their kind hospitality and continued support of visiting naturalists to the Philippines.

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COLOR PLATE

The Frontispiece painting by John A. Ruthven has been made possible by an endowment established by George Miksch Sutton.

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SEASONAL DISTRIBUTION OF THE AZURE GALLINULE (*PORPHYRULA FLAVIROSTRIS*), WITH COMMENTS ON VAGRANCY IN RAILS AND GALLINULES

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Abstract.—Specimen records and field observations of the Azure Gallinule (*Porphyrula flavirostris*) provide evidence that this species undergoes seasonal movements in portions of its range. Although present year-round in much of Amazonia, it is seasonal in the Guianas, southwestern Amazonia, and Paraguay. Data from single localities within these areas also indicate that this species is seasonal. The existence of five extralimital records supports the hypothesis that this species is migratory. Presence may be timed to correspond with wet or high-water seasons. Unfortunately, the absence of label data on gonad size and fat deposits for the vast majority of the 143 available specimens limits their use in unravelling the seasonal cycle of this species. The preferred habitat of the Azure Gallinule in western Amazonia is extensive areas of marsh grass (*Paspalum*). An overview of rail and gallinule distribution emphasizes that many species may occur at unpredictable times and places, as might be predicted from their dependence on ephemeral marsh habitats. The two congeners of the Azure Gallinule, Purple and Allen's gallinules (*P. martinica* and *P. alleni*), provide extreme examples of species capable of long-distance, extralimital occurrences. From these points, we conclude that the recent New York (USA) specimen of Azure Gallinule is best regarded as a record of a wild bird. *Received 4 Aug. 1989, accepted 1 Nov. 1989.*

The Azure Gallinule (*Porphyrula flavirostris*) is found in the lowland tropics of South America, primarily in the Amazonia-Guianas region. Until the recent specimen record from New York (Boyle et al. 1987), this species had not been found farther north than Venezuela, Trinidad, Guyana, and Surinam. Most current references (e.g., Meyer de Schauensee 1966, Haverschmidt 1968, Blake 1977, Ripley 1977, Meyer de Schauensee and Phelps 1978, Sick 1985) indicate or assume implicitly that this species is completely sedentary. Therefore, whether the recent record from New York represented a wild bird has been controversial (Blom 1987, Boyle et al. 1987). Because our own field experience with the Azure Gallinule in Peru (Parker 1982, unpubl. data) and Colombia (JVR, unpubl. data) suggested that this species was present at certain localities only seasonally, we suspected that a thorough analysis of specimen records might reveal seasonal movements. Here we analyze the geographic and seasonal distribution of the Azure Gallinule, evaluate the New York record, and summarize the evidence that some species of rails and gallinules are champion long-distance dispersers.

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METHODS

We solicited specimen data from most museums with extensive holdings of Amazonian birds. Reliance on specimen records to determine seasonal distribution has obvious drawbacks, particularly for analysis of a marsh-dwelling species that occurs in a relatively little-known region. Absence of specimens from a region or a season might mean only that the region was not visited by a collector of marsh birds at that season or that the collector was unable to secure a specimen. Also, the number of specimens collected may not be related to a species' abundance. For example, S. L. Klages' field notes indicated that the Azure Gallinule was "plentiful" at Santarem, yet he collected only two specimens during his six months there (K. C. Parkes, in litt.).

To control in part for possible seasonal and regional biases in collecting effort, we also requested similar data from certain museums for another species of Amazonian marsh bird, the Wattled Jacana (*Jacana jacana*); our (untested) assumption was that the Wattled Jacana is sedentary. Although the Purple Gallinule (*Porphyrula martinica*) might be considered a more appropriate species for comparison because it is ecologically and taxonomically closer to the Azure Gallinule and occurs throughout its range, we did not do so because: (1) Amazonian populations of the Purple Gallinules may be comprised of individuals that are migrants from both North America and southern South America, and (2) Amazonian breeding populations might also be migratory.

We placed each specimen record in one of five regions of South America: (1) the Guianas (Guyana, Surinam, French Guiana); (2) eastern Amazonian Brazil (Pará, Amapá); (3) western Amazonia (western Brazil in Amazonas, southern Venezuela, Amazonian Colombia and Ecuador, northeastern Peru in Loreto); (4) southwestern Amazonia (southeastern Peru in Madre de Dios, eastern Bolivia, southwestern Brazil in Mato Grosso); and (5) Paraguay. Two specimens from Minas Gerais, Brazil, and three from the Andes were not placed in any of these regions.

Wattled Jacanas were collected in 54 (90%) of the 60 month-samples in our five regions (Figs. 1–5), even though only a subset of the museums surveyed for Azure Gallinules were also surveyed for Wattled Jacanas. Furthermore, Azure Gallinules were collected in all six month-samples in which no Wattled Jacanas were collected. We interpret these results to indicate that the potential biases in the distribution of collecting effort in marsh habitats were not of the magnitude that would give us a completely erroneous view of the distribution of the Azure Gallinule. Nevertheless, we urge caution in interpretation of "negative" data, i.e., gaps in the specimen record. To augment our data base, we also searched the literature for additional records of Azure Gallinules as well as reports of seasonality in its distribution, and we extracted from our field notes all our sight records of this species.

RESULTS

General status, distribution, and habitat.—Reference works (Peters 1934, Meyer de Schauensee 1966, Haverschmidt 1968, Blake 1977, Ripley 1977, Meyer de Schauensee and Phelps 1978, Sick 1985) give conflicting information concerning the range of the Azure Gallinule; some describe the range as spotty, whereas others imply that it has a continuous distribution in Amazonia and its periphery. Only in Surinam has it been considered common (Haverschmidt 1968); we found only 1–4 specimen records each from countries in western Amazonia, i.e., Venezuela, Colombia, Ecuador, Peru, and Bolivia (Table 1).

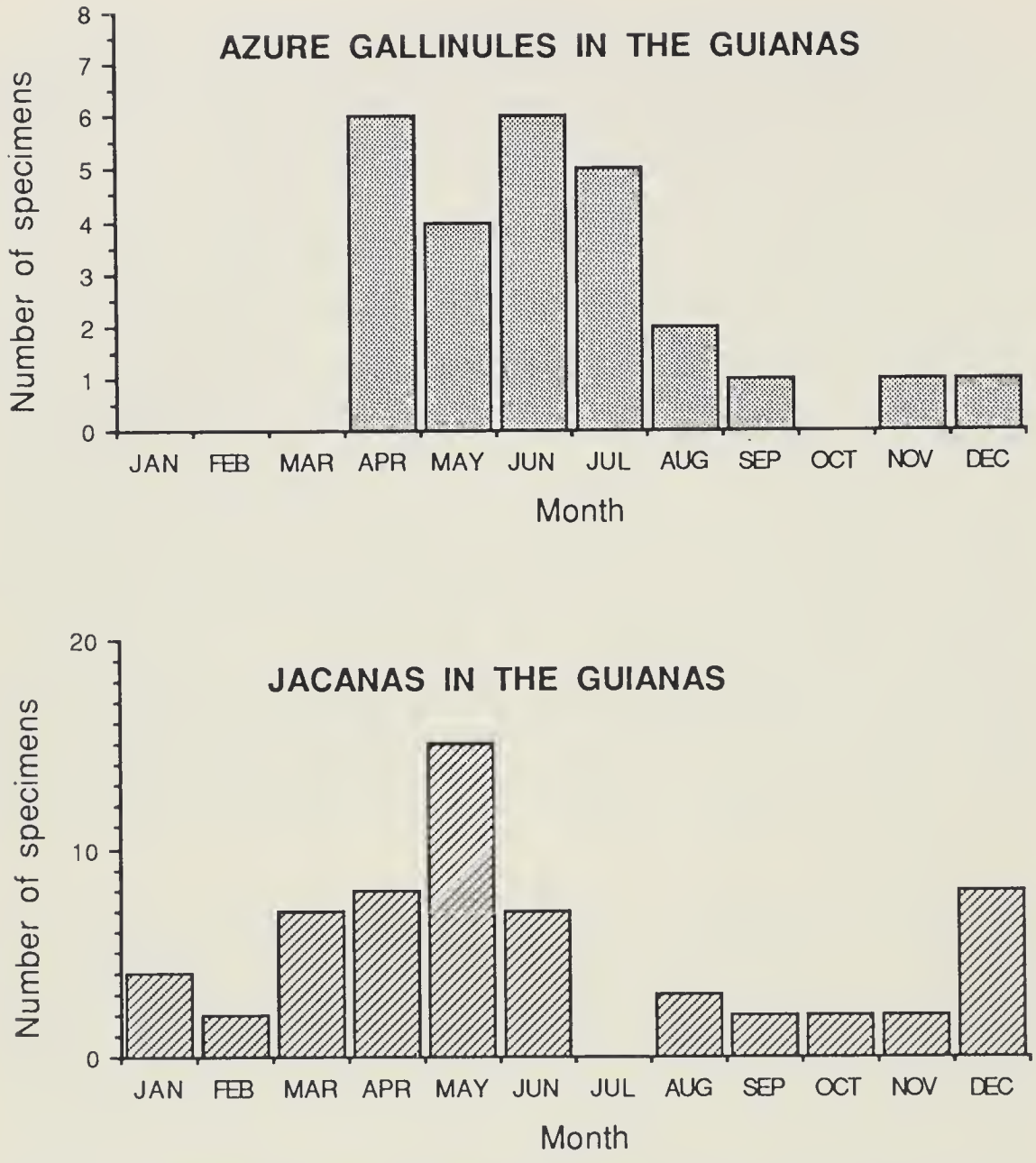

FIG. 1. Seasonal distribution of specimens of Azure Gallinule and Wattled Jacana in the Guianas.

Because most of these references relied in part on the same specimen data that form the backbone of our analysis, it is not surprising that our conclusions are generally similar. We suspect, however, that the Azure Gallinule is more widespread in Amazonia than specimen records indicate, because: (1) it is usually inconspicuous and its habitat is difficult to penetrate, and (2) immatures closely resemble immatures of the larger Purple Gallinule and therefore may be overlooked (Parker 1982).

Little has been published on the habitat of the Azure Gallinule. Haverschmidt (1968) stated that it is "common in freshwater swamps with deep

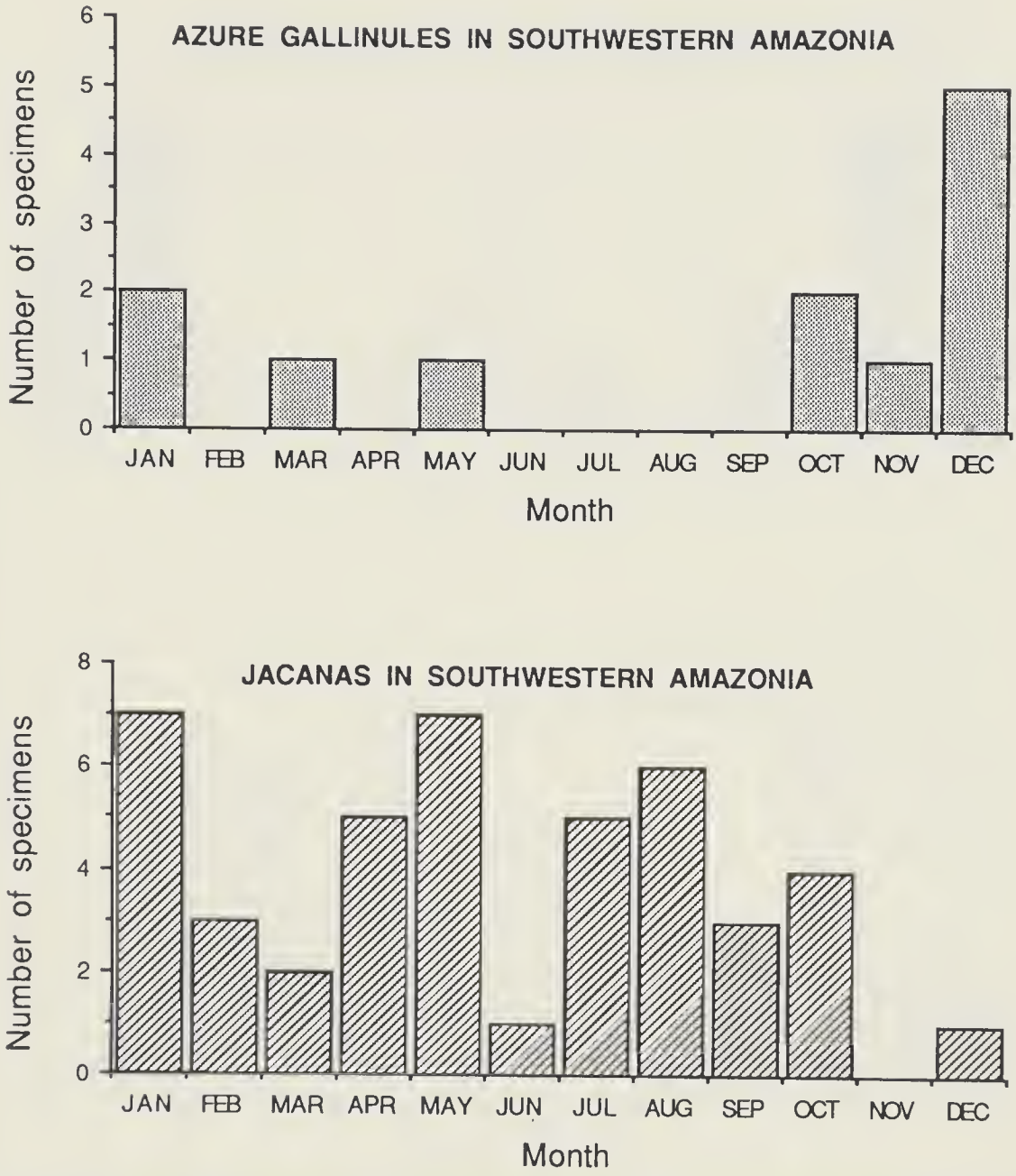

FIG. 2. Seasonal distribution of specimens of Azure Gallinule and Wattled Jacana in southwestern Amazonia.

water and a thick vegetation of grass, also in ricefields," and Hilty and Brown (1986) reported that it is "uncommon and local in freshwater marshes, ricefields, and marshy shores of ponds, lakes, and lagoons." In western Amazonia, we have found that the species inhabits floating mats of grasses and sedges along the edges of oxbow lakes (Parker 1982) and riverine marshes. Azure Gallinules are usually flushed from inundated grasses that rise 15–30 cm above water. They avoid (slightly drier?) areas with bushes and *Heliconia,* the preferred habitat of Purple Gallinules. When rivers are at or near flood stage, Azure Gallinules congregate in the

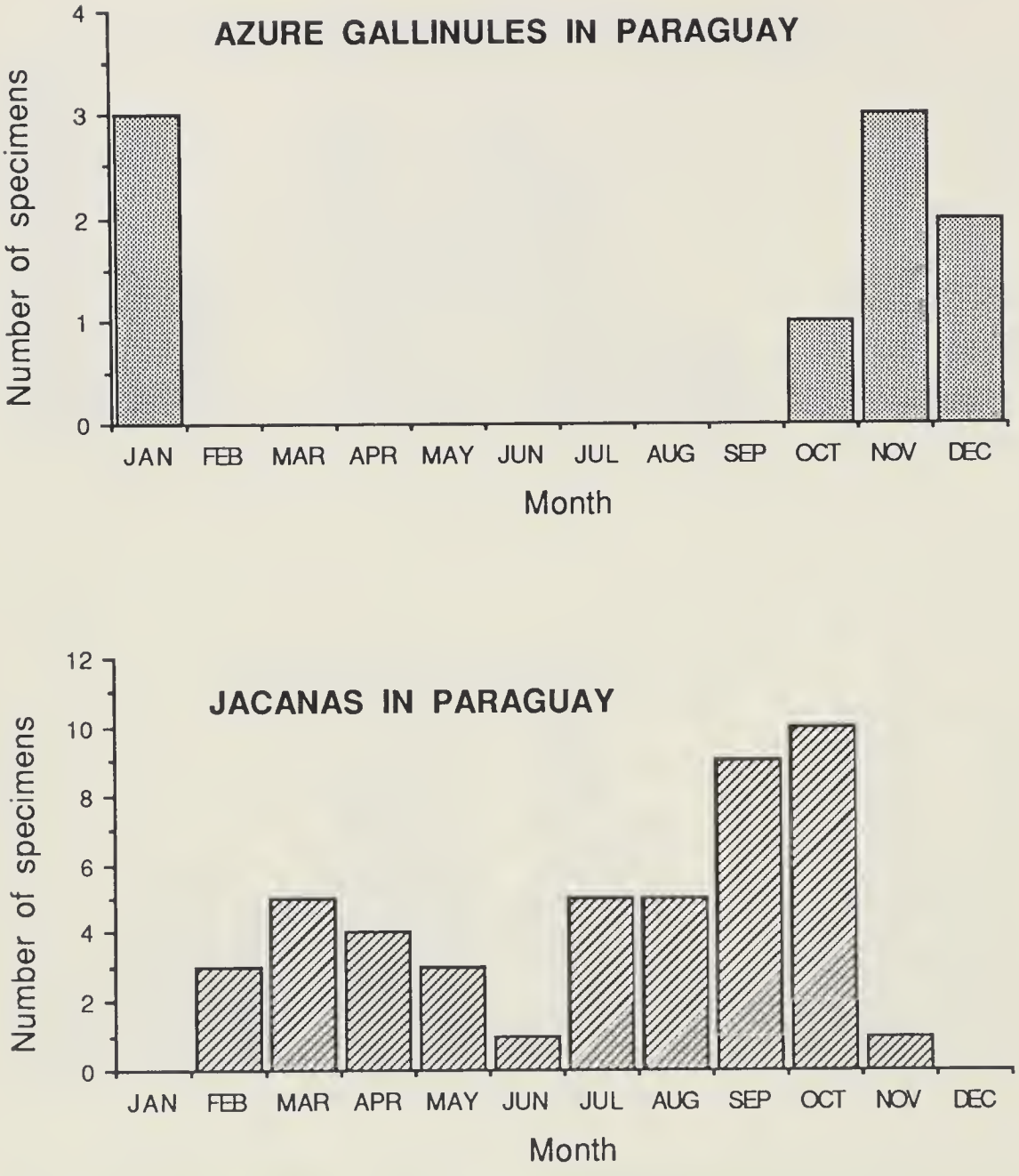

FIG. 3. Seasonal distribution of specimens of Azure Gallinule and Wattled Jacana in Paraguay.

grassy (*Paspalum*) marshes along the edges and lower ends of river islands; such areas occasionally cover up to 1 km^2, but are usually long and narrow. The birds usually stay hidden within *Paspalum* about 1 m tall, but when river-levels are near flood stage, Azure Gallinules occasionally perch near the tops of grass clumps. Under these conditions, "a minimum of 12 (and prob. 15–16)" Azure Gallinules were observed at Isla Corea and Quebrada Tucuchira near Leticia, Colombia, 20–23 February 1984 (S. L. Hilty and R. S. Ridgely), and six (all immatures) were flushed from ca 15 cm of

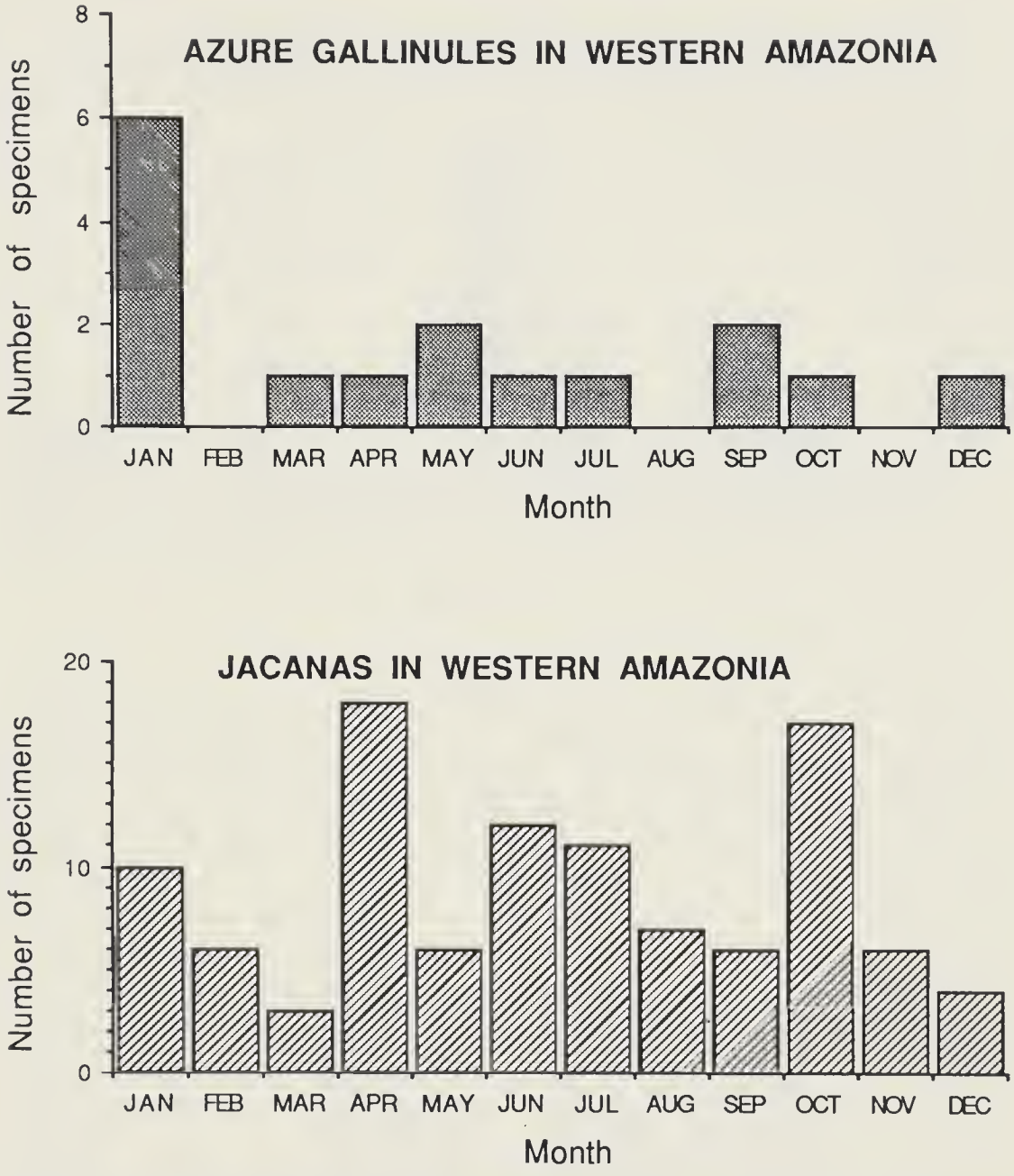

FIG. 4. Seasonal distribution of specimens of Azure Gallinule and Wattled Jacana in western Amazonia.

grass over 1 m of water along a river channel through Isla Timicurillo below Iquitos, Peru, on 27 January 1989 (Parker and T. S. Schulenberg). Six additional records of single, immature gallinules flushed from flooded *Paspalum* areas on river islands in the lower Rio Napo (Isla Llachapa, Isla Tamanco) range from January to July (Parker pers. obs.). At Quebrada Tucuchira and nearby Isla de Santa Sofía II, Remsen found 1–4 Azure Gallinules in extensive *Paspalum* mats on eight dates from 21 May to 24 June (1975), near the peak flood stage of the Amazon River. Until such

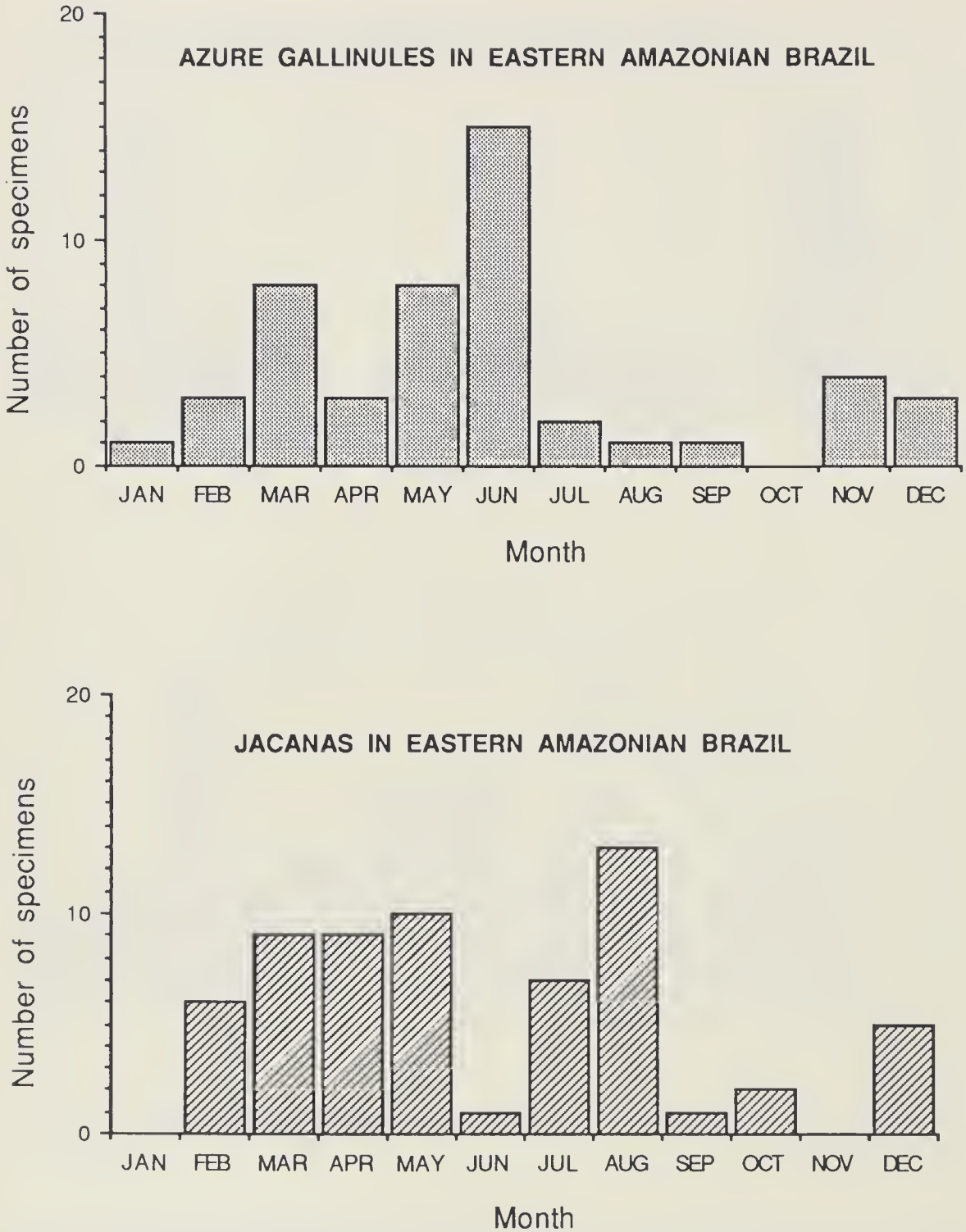

FIG. 5. Seasonal distribution of specimens of Azure Gallinule and Wattled Jacana in eastern Amazonian Brazil.

habitats are thoroughly surveyed, our knowledge of the true status of Azure Gallinule will remain incomplete.

The distribution of specimen records of the Azure Gallinule suggests that it is more common in forested regions than in the wet savanna regions

TABLE 1
NUMBER OF AZURE GALLINULE SPECIMENS FROM EACH COUNTRY

Country	Number of specimens
Bolivia	4
Brazil	84
Colombia	4
Ecuador	3
Guyana	9
Paraguay	9
Peru	1
Surinam	22
Venezuela	2
United States	1
Unknown	3

bordering Amazonia, in spite of the abundance of marsh habitat in these savannas. We found only one specimen record from the savannas (*llanos*) region of eastern Colombia and northern Venezuela, although Thomas's (1979) records from the Venezuelan *llanos* and McKay's (1980) records from the edge of the Colombian *llanos* suggest that the absence of specimen records is misleading. Likewise, there are few records from the wet savannas (*pantanal*) of eastern Bolivia and southwestern Brazil. However, we cannot tell how many of the specimens from the Guianas and eastern Amazonian Brazil were taken in the wet savannas within these generally forested regions.

Because we surveyed most of the world's collections containing Amazonian birds (see Acknowledgments), we think that we have located >75% of the extant specimens. Therefore, the low number of specimens (143) suggests that it is either not a common species, that it is difficult to collect, or (as we suspect) both. In contrast, there are more than twice as many specimens of Wattled Jacana in the American Museum of Natural History alone. Our own fieldwork confirms that the Azure Gallinule is definitely not a common bird in southeastern Colombia, eastern Peru, or northern Bolivia, areas from which relatively few specimens are known (Table 1). Specimen records suggest that the Azure Gallinule is most common in Surinam and eastern Amazonian Brazil, particularly in the state of Pará; however, Pará is an area worked intensively by collectors in Brazil, and thus the large number of specimens from there may reflect a regional bias in collecting efforts.

Seasonal distribution.—The Azure Gallinule is highly seasonal in occurrence in three regions. In the Guianas (Fig. 1), almost all records are from April to August, the wet season, with one immature from November and an adult from December. In contrast, most records from southwestern Amazonia (Fig. 2) are from October to January, except for one March (adult) and one May (immature) specimen and a few other sight records of immatures from June to August by Parker (1982). In Paraguay (Fig. 3), all records are also from October to January, the wet season there. In the two regions closest to the equator, western Amazonia (Fig. 4) and eastern Amazonian Brazil (Fig. 5), seasonality in distribution of specimen records is not so pronounced, but evident nonetheless. In eastern Amazonian Brazil, all but nine specimens (18%) were collected from February to August; of these nine, five were immatures. In western Amazonia, specimens are relatively evenly distributed throughout the year, except for a notable increase in January. Over all, the species is present seasonally in areas at the periphery of its range, but seasonality is less evident in the Amazonian regions closest to the equator. ffrench (1985) reported that there were a "considerable number" of sight records from Nariva Swamp, Trinidad, all since 1978, but did not indicate whether there was a seasonal pattern.

Along the upper Amazon River near Iquitos and Leticia, we have found that the presence of Azure Gallinules in *Paspalum* marshes coincides with the high river levels there from January to July. From late July to early December this habitat is usually one to several meters above water level. Remsen worked nearly daily in the vicinity of *Paspalum* marshes near Leticia for nine months in two field seasons spanning 18 May to 21 November, but Azure Gallinules were detected no later than 24 June. Where these individuals go from July to December is mysterious, especially because the distribution of specimens show little seasonality in the region as a whole (Fig. 4).

The monthly distribution of specimen records of Wattled Jacana in the Guianas (Fig. 1) shows a peak similar to that of Azure Gallinule in April–June, but otherwise is less seasonal. In southwestern Amazonia (Fig. 2), Wattled Jacanas have been collected year-round, with lows in November and December; this contrasts with the strongly seasonal pattern of Azure Gallinules in the same region (Fig. 2). In Paraguay, the jacana may be seasonal in occurrence (Fig. 3), but the period of scarcity there, November through January, corresponds to the period of presence of Azure Gallinule (Fig. 3). In western Amazonia (Fig. 4), the monthly distribution of jacana specimens is relatively even, as it is in the Azure Gallinule. In eastern Amazonian Brazil, the monthly distribution of the jacana is also similar

to that of Azure Gallinule (Fig. 5), with some seasonality (relatively scarce from September through January) evident in both species.

In summary, the monthly distribution patterns of specimen records of the largely sedentary Wattled Jacana support our interpretations of seasonality in distribution of the Azure Gallinule. In the Guianas, southwestern Amazonia, and Paraguay, where the Azure Gallinule is highly seasonal, the Wattled Jacana is not seasonal or shows a different pattern of seasonality. In the regions in which the presence of Azure Gallinule appears to be less seasonal or aseasonal, the Wattled Jacana shows a similar pattern.

Evidence for migration.—Although seasonal distribution of specimen records may provide circumstantial evidence for migration, more direct evidence will come from year-round surveys from single localities. Unfortunately, such surveys are nearly nonexistent within the range of the Azure Gallinule. Nevertheless, evidence from those few localities indicates that this species is present only seasonally. At the well-worked Tambopata Reserve in Dpto. Madre de Dios, Peru, Parker et al. (1982) found that small numbers appeared in early November and were present through at least January. At another site in Madre de Dios, Terborgh et al. (1984) considered Azure Gallinule to be a migrant (but in a different period, roughly March–October); however, there may be only one definite record from that site, an immature seen on 3 January 1982, and the species may actually be absent there from at least June to at least December (S. K. Robinson and D. Willard, unpubl. data). In western Dpto. Meta, Colombia, Azure Gallinules were present only from late May to mid-July in two successive years (W. McKay data in Hilty and Brown 1986). At a locality in the llanos of Venezuela, Thomas (1979) found this species present only from August to December.

Extralimital records and records in inappropriate habitat also provide circumstantial evidence for migration (or at least capability of long-distance movement). We are aware of five such records for the Azure Gallinule. An immature was collected at Escorial, at 3000 m in the Andes of Mérida, Venezuela, on 24 October 1903 (American Museum of Natural History). A specimen was found in a residential garden within the city of Bogotá, Colombia, ca 2600 m, on 9 December 1958 (Nicéforo and Olivares 1965, Olivares 1969) and another was obtained in the city of Bogotá on 2 December 1965 (Olivares 1969). John Coons and John Arvin (in litt.) saw an adult on 8 January 1989 in southern Venezuela sitting in a bush on "an otherwise unvegetated granite dome that formed part of an extensive escarpment that looked out over the canopy of miles of unbroken lowland forest" with "nothing remotely resembling gallinule habitat

for many miles in any direction." Arvin remarked that "the bird was much as one might occasionally find a migrant Purple Gallinule totally lost in some backyard or city park." This bird was found at 490 m elevation at about Km 110 on the highway that climbs up to the Gran Sabana, between El Dorado and Santa Elena on the Brazilian border. Finally, Parker saw an adult on 26 November 1986 in a flooded (short-grass) pasture near extensive *Typha* reedbeds, 1 km south of the Taim Ecological Station (32°30′S Lat., 52°35′W Long.), Rio Grande do Sul, Brazil, approximately 800 km SSE of the nearest previous record. We believe that these records represent wandering or migrating individuals.

Presence of large subcutaneous fat deposits would also provide strong evidence for migration. Unfortunately, most specimens of Azure Gallinule were collected decades ago (Fig. 6), before most study skins were accompanied by extensive data on fat, molt, and reproductive condition. In fact, so few specimens of Azure Gallinules were accompanied by data on subcutaneous fat that an analysis was not possible. A specimen labelled as being "fat" was taken in December in Guyana, and a specimen labelled as having "moderate fat" was taken in October in Ecuador.

We note that if only half the specimens of Azure Gallinule were accompanied by gonad, molt, and fat data, unravelling this species' annual cycle would have been relatively easy. Unfortunately, we suspect that this species is not unusual in having the vast majority of specimens collected before such data were included as standard label data.

Evidence of breeding.—Haverschmidt's (1968) summary of nesting information in Surinam covered three nests, all with eggs: 22 May, 15 June, and 9 August. These are the only published accounts of breeding that we have been able to find. Teixeira and Best (1981) reported that in Amapá, eastern Amazonian Brazil, the local residents claimed that the Azure Gallinule nested in May and June. There are apparently no egg sets in the world's museum collections (L. Kiff, in litt.); the egg set for Azure Gallinule in the Museum of Vertebrate Zoology listed by Kiff and Hough (1985) is an error (N. K. Johnson, in litt.).

Gonad data on labels of museum specimens can often be extremely useful for analyzing the timing of breeding of tropical species for which few nests have been discovered. Unfortunately, of the 96 specimens of adults, only 12 have label data on reproductive condition. Of these, only five have measurements of gonads; the rest have only abbreviations or codes, such as "ov. enl.," that are unfortunately subjective or ambiguous (Marra, in press). The seven birds in breeding condition are: (1) four from March, three from Pará and one from Amazonas, Brazil, and (2) three from Amazonian Ecuador, one in June (egg in oviduct), one in July, and

FIG. 6. Chronological distribution of Azure Gallinule specimens.

one in October (the latter a male with testes 11 × 6 mm, but with heavy general body molt and moderate fat, suggesting that it may not have been actively breeding). The five not in breeding condition are two from September from Amazonas, Brazil, one from November from Beni, Bolivia, and two from December from Pará.

Although generalization from such a small sample is obviously risky, the nearly complementary monthly distribution of reproductive and nonreproductive individuals suggest that the breeding season extends from March to August, and possibly as late as October, and that the nonbreeding season extends from September through December. These same data indicate that the Azure Gallinule breeds in the two areas where present year-round (western Amazonia and eastern Amazonian Brazil) and in one area where present only seasonally (Guianas).

The three breeding records from Surinam fall within the wettest period of the year, April–August (Haverschmidt 1968, p. xvi). Azure Gallinules in reproductive condition were taken in upper and lower Amazonian localities in March, June, July, and October; such seasonality may correspond to high river and lake levels rather than to local rainfall patterns. There is little seasonality in rainfall along the upper Amazon.

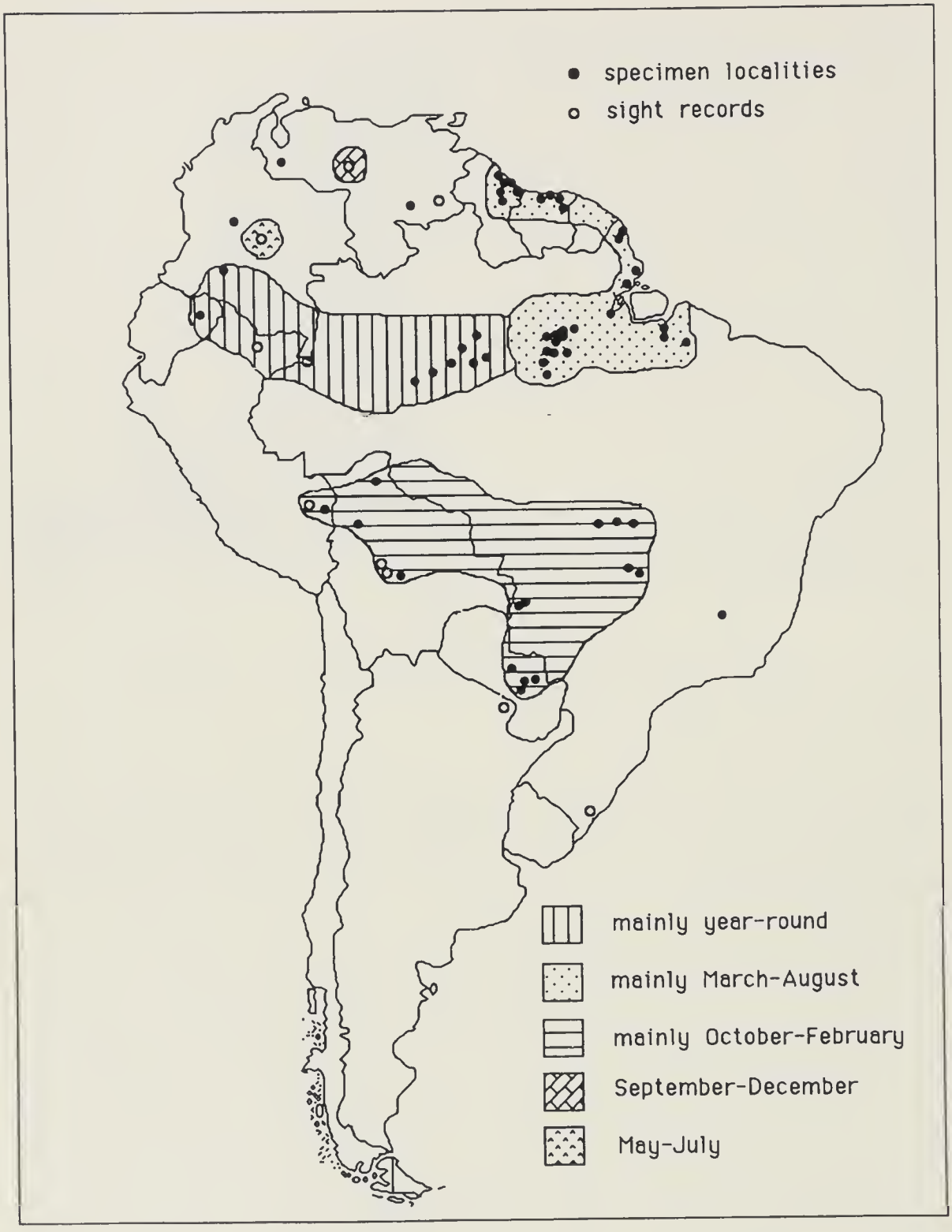

FIG. 7. Synthesis of seasonal distribution of Azure Gallinule in South America. Shaded areas indicate areas of regular occurrence. Isolated localities represent those considered to be extralimital (N = 4; see text) or difficult to assign to a region: (1) a specimen record for Chanaro River, (Bolivar?), Venezuela, is undated and cannot be included comfortably within any shaded region; (2) two specimens from Lagoa Santa, Minas Gerais, Brazil (4 April 1866, 9 Sept. 1839), may belong within the southwestern Amazonia-Paraguay cluster of localities; and (3) a sight record from Formosa, Argentina, probably also belongs within the Paraguay

Age and sex distribution.—Of the 126 sexed specimens, 74 (59%) are males. Within regions, sex ratios do not differ significantly from the overall sex ratio. In southwestern Amazonia, females outnumber males 7:5, but this sex ratio is not significantly different from that of the other individuals in the other regions combined ($\chi^2 = 0.13$, $P > 0.70$).

Of 113 specimens aged by plumage characters (blue-necked = adults, buff-necked = immatures), 96 (85%) were adults. Specimens in immature plumage (with dates) have been taken in May (N = 2), June (6), Sept. (1), Oct. (1), Nov. (3), and Dec. (2). Ten of the 16 immatures were collected in eastern Amazonian Brazil. Although specimens of immatures are too few to provide insights into their seasonal or geographical distribution, they form a disproportionately large proportion of the odd seasonal records within the various regions (see Seasonal Distribution). Although the vast majority of specimens are adults, most of our sight records are of immatures; we have no explanation for this difference.

DISCUSSION

We interpret the pattern of seasonal distribution of records to indicate that the Azure Gallinule is migratory, at least in part of its range. With the complimentarity in seasonal distribution between northeastern South America (the Guianas, and to some extent eastern Amazonian Brazil) and the southern periphery of Amazonia (southwestern Amazonia and Paraguay), we hypothesize that most of the population in northern South America disperses southward (after breeding May–July) to the southern periphery of Amazonia, where the nonbreeding season (the austral summer and wet season) is spent, and then the population returns to northeastern South America in February and March (Fig. 7). Such a migration route is approximately 1800 km long. This interpretation clearly must be viewed with caution because: (1) the number of breeding records is small, (2) year-round surveys from critical localities are nearly nonexistent, and (3) in general, marsh habitats in Amazonian South America are visited infrequently by ornithologists.

The specimen from New York was obtained on 14 December. From our hypothesis outlined above, this corresponds to the season when most

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cluster of localities. We were unable to locate any specimens from French Guiana other than two specimens labelled only "Caycnne." Thc reason that there are far fewer specimen localities plotted than there are specimens are that (1) in several cases, numerous specimens have been taken from the same locality, and (2) a number of localities in Brazil could not be located. Sight records from Trinidad (ffrcnch 1985) were not plotted because dates were given for only one record (July).

of the population has left northern South America for the southern periphery of Amazonia. The most likely date, therefore, for a vagrant would be during the periods August–December or January–February. In fact, the five other records that clearly represent vagrant individuals are from this period: the specimen from the high Andes of Venezuela was from late October, the sight record from Rio Grande do Sul was from November, the two specimens from the Andes of Colombia were from December, and the sight record from the Gran Sabana was from January. Therefore, the December record for New York falls within the period during which vagrants have been detected and during the presumed nonbreeding season. Of unknown relevance is the observation that the North American records of other tropical rallids (Paint-billed Crake [*Neocrex erythrops*] and Spotted Rail [*Pardirallus maculatus*]; Arnold 1978, Parkes et al. 1978, Blem 1980) were from November, December, and February, thereby bracketing the Azure Gallinule record. If the Azure Gallinule specimen from New York were an immature instead of an adult, then the case for the New York record representing a wild bird might also be considered stronger; however, at least two of the five records of vagrant Azure Gallinules have been of adults. The New York specimen did not have large subcutaneous fat deposits and was not emaciated.

We think that the New York record should be regarded as a natural vagrant, for the following reasons. First, the evidence favors treatment of the Azure Gallinule as a migratory species, at least in part of its range, and, as we will develop below, migratory rallids can be expected to appear at unpredictable places and seasons. Second, the dates of the extralimital records of Azure Gallinule show that vagrants can be expected from October to January, thereby bracketing the December date for the New York specimen. Third, the specimen apparently showed no signs of having been in captivity, and Azure Gallinule is virtually unknown in captivity. In our opinion, therefore, the New York specimen should be regarded as a valid record of a wild bird until proven otherwise. We also think that other North American records of tropical rails (Spotted Rail; Parkes et al. 1978; and Paint-billed Crake; Arnold 1978, Blem 1980) should also be regarded as representing natural vagrants. Although, in contrast to Azure Gallinule, there is no evidence that these two species are migratory, neither is there any evidence for the individual specimens having been in captivity (e.g., abnormal wearing of plumage, feet, or bill), or of those species ever being kept in captivity. We think that the statements by the AOU (1983) in reference to these records that "some of these individuals may have been transported by man" and "the North American vagrants may have been man-assisted" are overly conservative and ignore the propensity of rails to occur as vagrants at unexpected times and places.

In North America, for example, migratory rallids have produced the following extralimital records (from AOU 1983): Corn Crake (*Crex crex*) in seven states, two Canadian provinces, and Bermuda; Spotted Crake (*Porzana porzana*) in the Lesser Antilles; Black Rail (*Laterallus jamaicensis*) in Bermuda; King Rail (*Rallus elegans*) in Newfoundland; Virginia Rail (*R. limicola*) in Bermuda and Greenland; and Common Moorhen (*Gallinula chloropus*) in Newfoundland, Greenland, Iceland, and the Commander Islands. Among species generally considered sedentary, the following records are of interest: (1) Paint-billed Crake in Texas (*N. e. erythrops* of the Galapagos and western Peru; Arnold 1978), Virginia (probably *N. e. olivascens* of eastern South America; Blem 1980), at ca 2600 m in the streets of Bogotá, Colombia (Olivares 1969), and at 3375 m in a garden in a suburb of La Paz, Bolivia (Remsen and Traylor 1983); Spotted Rail in Pennsylvania (as well as the Juan Fernandez Islands, 650 km from the Chilean mainland and at least 1500 km from the nearest potential breeding population; Parkes et al. 1978); and Clapper Rail (*R. longirostris* in Newfoundland, Vermont, Nebraska, western Pennsylvania, and West Virginia; AOU 1983, Mulvihill and Leberman 1989).

As noted by Parkes et al. (1978), perhaps the champion vagrant among the rails and gallinules is a species in the same genus as the Azure Gallinule, the Purple Gallinule. The AOU (1983) listed records of Purple Gallinules from the following extralimital localities: South Africa (at least 20 records; Urban et al. 1986), the Azores, Britain, continental Europe, Falkland Islands, Tristan da Cunha Is. (ca 3800 km from South American mainland), Ascension Is. (ca 2500 km east of South American mainland), the Galapagos Islands, St. Helena Is. (ca 6400 km from the South American mainland), and in North America, as far west as California and as far northeast as Labrador. The third species in the genus *Porphyrula,* Allen's Gallinule (*P. alleni*) of sub-Saharan Africa, has been recorded in Europe, North Africa, and on offshore islands as follows (from Cramp et al. 1980, Urban et al. 1986): Britain (N = 1), France (2), Spain (2), Denmark (1), W. Germany (1), Italy (5), Cyprus (1), Egypt (1), Tunisia (1), Morocco (4), the Azores (4), Ascension Is., St. Helena Is., Comoro Is., and Rodriguez Is. (In fact, we wonder whether Allen's Gallinule was eliminated from consideration in all extralimital sight records of the superficially similar Purple Gallinule; it seems inevitable that Allen's Gallinule will eventually be recorded in the New World.) Furthermore, Allen's Gallinule is known to be an intratropical migrant in Africa, with migrations in response to wet and dry seasons; it arrives in an area at the onset of the wet season, breeds, and then leaves during the dry season (Urban et al. 1986). We suspect that Azure Gallinule performs similar intratropical migrations in response to wet and dry seasons in South America.

Because most rails are secretive or prefer concealing habitats, they are more difficult to detect than most kinds of birds. Therefore, we feel that knowledge of seasonal movements and patterns of vagrancy in rails is at a primitive stage relative to that for other bird groups. We speculate that the number of vagrant records of these birds would increase dramatically if ornithologists were able to sample more effectively the emergent vegetation and tall wet grass that is the preferred habitat for most rails. It is, therefore, not surprising to us that many extralimital records of rallids were obtained from TV and other towers, mammal traps, cats, and by other methods that do not include the usual activities of ornithologists or birders.

A global overview of rail and gallinule distribution patterns also provides evidence for the dispersal capabilities of these birds. Rails and gallinules in general are among the best long-distance island-colonizers among nonmarine birds (Ripley 1977:15–20). Many remote, oceanic islands have been colonized by one or more species of rails. From the species accounts in Ripley (1977), we counted at least 15 species of rails and gallinules endemic to oceanic islands, and at least 10 other species that have from one to eight subspecies restricted to an oceanic island. Even these impressive tallies are almost certainly drastic underestimates of true rail diversity on islands. As Olson (1973, 1989), Olson and James (1982), and others have shown, many species of rails endemic to islands have disappeared recently (presumably exterminated by the arrival of humans and their commensal mammals) and are known only as neofossils. For example, Olson and James (1982) listed eight species of rails, all extinct, from recent fossils in the Hawaiian Islands. Further evidence for the dispersal capabilities of certain rallids comes from the amazingly widespread distribution of some species. For example, the Common Moorhen is found nearly world-wide, including on such remote oceanic archipelagos as Hawaii, the Galapagos, and the Marianas. That the Rallidae are excellent transoceanic dispersers is also suggested by the unusual distribution patterns of rallid genera—many have nearly world-wide distributions or at least pantropical distributions, in glaring contrast to the pattern shown by most nonmarine, nonboreally distributed birds. For example, *Porzana* (including the Sora of North America) is found in Africa, Madagascar, Asia, Australasia, New Zealand, most Pacific Islands (including Hawaii), North America, the West Indies, South America, and Asia. Finally, even within a species, several dramatically disjunct distributions suggest long-distance colonizing ability (although vicariance could also potentially explain such a pattern). For example, there is a population of the Yellow Rail in the highlands of Mexico and populations of the Black Rail and the Virginia Rail in western South America (Ripley 1977).

In summary, because rails and gallinules account for some spectacular instances of vagrancy, with some records thousands of kilometers from their known breeding range, and because their global distribution pattern indicates that they are champion dispersers and colonizers, we think that extralimital records of these birds should be regarded in general as representing wild vagrants unless there is some specific reason to think otherwise.

Why are some rails and gallinules such good dispersers? The essentially ephemeral nature of the marsh and wet grassland habitats of many species dictates that they must be good dispersers. Populations not capable of evacuating marshes that dry up in order to find new marshes are doomed to extinction. Most freshwater marshes proceed through various successional stages, the last of which is dry land. So, marsh birds have to be good dispersers, even if not migratory. Because their dispersal may be dictated by droughts, floods, and short-term successional stages, we also predict that their pattern of seasonal occurrence would be somewhat erratic (other than migration periods for those that are long-distance migrants). Therefore, we predict, a priori, that species thought to be sedentary may appear at unpredictable times and places. Also, the "weak" flight of many rails and gallinules may make them particularly vulnerable to being blown off-course by storms.

Although several taxa of rallids are excellent dispersers, many taxa, as pointed out to us by S. L. Olson (in litt.), are not. Numerous species and genera are confined to restricted regions of the tropics, with no history of dispersal or vagrancy. As a corollary of our arguments above, we predict that those species least likely to occur as vagrants are those restricted to forests and other habitats that show much less seasonal or annual variation in their suitability than marshes.

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WINTER DISTRIBUTION OF PIPING PLOVERS ALONG THE ATLANTIC AND GULF COASTS OF THE UNITED STATES

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ABSTRACT.—We conducted winter surveys of Piping Plovers (*Charadrius melodus*) along the Atlantic Coast (December 1986–March 1987) and Gulf Coast (December 1987–March 1988) of the United States to identify specific wintering sites. A total of 222 Piping Plovers was observed on the Atlantic Coast (about 14% of the entire Atlantic Coast breeding population) and 1508 on the Gulf Coast (about 56% of the entire Great Lakes/Northern Great Plains breeding population). Highest Atlantic Coast estimates occurred in Georgia (N = 105; 47.5%), whereas the most plovers on the Gulf Coast occurred in Texas (N = 834; 55.3%). The survey included 1422 km of barrier beach on the Atlantic Coast (69% of the coast) and 1283 km on the Gulf Coast (50% of the coast). The greatest potential for locating more plovers in the United States is in South Carolina and Louisiana. However, a large percentage of the North American breeding population (particularly on the Atlantic Coast) probably winters outside the United States, thus future surveys should explore the Caribbean and Mexico. *Received 28 April 1989, accepted 21 Nov. 1989.*

The Piping Plover (*Charadrius melodus*) is a migratory shorebird endemic to North America, which was designated as threatened/endangered in 1986 (Federal Register 1985). Piping Plovers breed along the Atlantic Coast from Maritime Canada to North Carolina, along the Great Lakes, and in the northern Great Plains of Canada and the United States (Johnsgard 1981, Haig and Oring 1985). The primary winter range is along the Atlantic and Gulf Coasts from North Carolina to Mexico (Haig and Oring 1985).

Knowledge of the winter distribution of migratory shorebirds is important because substantial mortality can occur during this portion of their annual cycle (Baker and Baker 1973, Evans 1976, Myers 1980). Such data are especially important for Piping Plovers because they can spend 7–8 months per year away from breeding areas (Haig and Oring 1985). Research on breeding areas has contributed knowledge of demographics (Wilcox 1959, Haig and Oring 1988a, b), behavior (Cairns 1982), and reproductive activity (Gaines and Ryan 1988, Haig and Oring 1988a). However, studies of wintering plovers are few (Haig and Oring 1985, Johnson and Baldassarre 1988).

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Haig and Oring (1985) conducted winter distribution surveys in 1983 along the Texas coastline and in 1984 along 1228 km of Gulf Coast beaches from Mexico to Florida. Although these surveys were the first on-site assessments of winter populations, they tallied only 25% of the total breeding population. Further, the Atlantic Coast portion of the winter range was not surveyed.

A comprehensive conservation plan for the Piping Plover must incorporate strategies addressing winter habitat. However, such strategies cannot be developed until winter distribution is delineated. Indeed, the Atlantic and Great Lakes/Northern Great Plains Recovery Plans for Piping Plovers include the determination of winter status and distribution as high priorities relative to population recovery efforts for this species (Dyer et al. 1987, Haig et al. 1988). The primary objective of our study was to provide a more accurate estimate of the distribution of Piping Plovers wintering in the United States.

METHODS

We determined winter distribution of Piping Plovers by surveying suitable habitat along the Atlantic Coast from Virginia to Key West, Florida (15 December 1986–15 March 1987), and along the Gulf Coast from Everglades National Park, Florida, to Brownsville, Texas (4 December 1987–23 March 1988). Survey sites were selected based on previous sighting records such as Christmas Bird Counts (CBC), historical accounts and recommendations from reliable sources (e.g., state biologists, Natural Heritage Program personnel, bird club members). We also distributed a flyer (Nicholls 1989) to various clubs, universities, and museums to publicize the survey and to request additional sighting information. Coastal ecological inventory maps (1:250,000; U.S. Fish and Wildlife Service 1982), topographic maps (1:24,000), and aerial and Landsat photographs also were analyzed to locate additional potential habitat. Thus, to increase the probability of locating major wintering sites, the survey deliberately focused on areas most likely to contain wintering Piping Plovers. Nicholls (1989) provides a detailed listing and associated maps of survey sites along both coasts.

Sites were surveyed by walking or driving a vehicle or 3-wheel all-terrain vehicle along the beach. Several islands and mudflats along intracoastal waterways were surveyed by boat. Aerial surveys of the Georgia coastline and the Ten Thousand Island and Big Bend regions of Florida were conducted to assess habitat potential in these less accessible areas. Less suitable areas of Piping Plover habitat (e.g., highly eroded and/or developed beaches) were checked by walking/driving 1-km sections of habitat every 1.6 km for sites 3–16 km long, every 4 km for sites 16–32 km long, and every 8 km for sites greater than 32 km. Thus, two coverage estimates were calculated: (1) the total km included in the survey (i.e., the total sampled area along the coastline), and (2) the total number of km actually walked or driven. Length of coastline (i.e., mainland and oceanside of islands) was determined from NOAA reports (National Oceanic and Atmospheric Administration 1979).

We counted Piping Plovers, using binoculars and a spotting scope. Double counting was not considered a problem because Piping Plovers generally occurred in small and/or discrete groups. Separate coastal estimates were made to represent the respective breeding populations because Haig and Oring (1988b) have demonstrated that Piping Plovers breeding on

the northern Great Plains and Great Lakes winter primarily along the Gulf Coast, whereas birds breeding along the Atlantic Coast winter farther south on the Atlantic.

We then quantified potential disturbance factors (e.g., human and off-road vehicle traffic, water and shoreline stabilization structures) and noted land ownership at each site. Finally, we rated each site (1 = highest) in importance to Piping Plovers based on the number of birds seen at the site and assessment of three habitat related criteria: (1) suitability of habitat (a subjective, comparative assessment of the quality and quantity of foraging and roosting area at the site), (2) CBC evidence of historical use, and (3) disturbance level, which was measured as either high or low/none, with a high level indicating potential threats to use of an area by plovers and/or imminent loss of habitat.

RESULTS

Atlantic Coast survey.—The Atlantic Coast survey covered 1422 km of coastline (659 km mainland and 763 km island) from the eastern shore of Virginia to the Florida Keys and examined 134 sites comprising 69% of the total coast; 41% of the coast actually was walked or driven. Survey coverage in each state ranged from 64–86%, and was highest in North Carolina (72%) and Georgia (86%) (Table 1). Sites with potential habitat but not included in the survey were Wreck, Ship Shoal, and Smith Islands in Virginia; Corncake Inlet on Bald Head Island, Brown and Bear Inlets at Camp LeJeune Marine Corps Base, and Tubbs Inlet at Waites Island in North Carolina; Cedar, Murphy, Dewee's, Capers, Morris, and Baypoint Islands in South Carolina; Little Tybee and Little Cumberland Islands in Georgia; and Cape Canaveral National Seashore and the Marquesas Keys in Florida.

We counted 222 Piping Plovers along the Atlantic Coast from North Carolina through Florida (Table 2). This represented about 5% of the total North American breeding population and 14% of the entire Atlantic Coast breeding population (Dyer et al. 1987), although a few Piping Plovers breeding on the northern Great Plains winter along the Atlantic Coast (Haig and Oring 1988b). Piping Plovers were found most frequently in Georgia (69.2% of the sites had birds) and least frequently in Florida (12.5% of the sites had birds) (Table 2). Georgia also had the highest density of plovers per km surveyed (0.77), followed by South Carolina (0.22). Individual sites with the highest numbers of Piping Plovers were Little St. Simon's Island (N = 32), Cumberland Island National Seashore (N = 20), and Pelican Spit (N = 19) in Georgia; Rachel Carson's Estuary (N = 16) in North Carolina; Huntington Beach State Park (N = 12) and North Island (N = 12) in South Carolina; and Shackleford Banks (N = 9) in North Carolina (Table 3). The remaining 30 sites with plovers had groups of <9 birds; mean group size was 6.

Sites with the highest plover numbers ranked a 1 or 2 and were considered the most important areas (Table 3). Importantly, 10 of these 12

TABLE 1

SURVEY COVERAGE OF THE ATLANTIC AND GULF COASTS, DECEMBER 1986–MARCH 1987

Coast State	Coverage				
	Percent of coast surveyed[a]	No. of sites surveyed	Mainland km[b]	Island km[c]	Percent of islands surveyed
Atlantic					
Virginia	66.1	12	29.6	88.8	69.4
North Carolina	72.2	31	46.4	301.6	82.9
South Carolina	63.6	22	85.6	105.4	58.2
Georgia	85.5	13	0.0	136.8	85.5
Florida	67.8	56	497.3	130.4[d]	72.2
Gulf					
Florida	43.8	94	212.5	326.8	73.7
Alabama	55.6	5	32.0	15.2	52.8
Mississippi	83.0	14	18.4	40.0	62.5
Louisiana	18.1	17	64.8	50.4	26.9
Texas	89.0	46	216.5	306.4[d]	80.6

[a] Percent of mainland and island barrier beach (NOAA 1979).
[b] Includes mainland barrier beach and coastal bay sites.
[c] Includes island barrier beach; estimates from Heritage Conservation and Recreation Service 1979.
[d] Does not include the Keys or barrier islands separated from the mainland by the intracoastal waterway.

TABLE 2

RESULTS OF THE PIPING PLOVER SURVEY ON THE ATLANTIC AND GULF COASTS, DECEMBER 1986–MARCH 1988

Coast State	Actual survey			Number per km		Sites with birds		
	Number of plovers	Percent survey total	Percent total population	Actual survey	Coast estimate	Number	Total sites visited	%
Atlantic								
Virginia	0	0	0	0	0	0	12	0
North Carolina	50	22.6	1.2	0.14	0.10	13	31	41.9
South Carolina	43	19.0	1.0	0.22	0.14	8	22	36.4
Georgia	105	47.5	2.5	0.77	0.66	9	13	69.2
Florida	24	10.9	0.6	0.04	0.03	7	56	12.5
Gulf								
Florida	351	23.3	8.4	0.66	0.28	32	94	34.0
Alabama	52	3.4	1.2	1.20	0.61	3	5	60.0
Mississippi	37	2.5	0.9	0.63	0.52	9	14	57.1
Louisiana	234	15.5	5.6	2.00	0.39	9	17	52.9
Texas	834	55.3	19.9	1.60	1.40	22	46	52.4

TABLE 3

IMPORTANT WINTERING SITES OF PIPING PLOVERS ALONG THE ATLANTIC COAST, DECEMBER 1986–MARCH 1987

State Site	Plovers surveyed: Number per site	Plovers surveyed: Percent of survey total	Importance rank[a,b]	Ownership
North Carolina				
Shackleford Banks	9	4.1	2	Federal
Rachel Carson's Estuary	16	7.2	1	Federal
South Carolina				
Huntington Beach State Park	12	5.4	2	State
North Island	12	5.4	2	State
Hunting Island State Park	8	3.6	2	State
Georgia				
Williamson Island	8	3.6	2	State
Blackbeard NWR	8	3.6	2	Federal
Little St. Simon's Island	32	14.5	1	Private
Pelican Spit	19	8.6	2	State
Cumberland Island				
National Seashore	20	9.0	1	Federal
Florida				
Anastasia State Recreation Area	6	2.7	2	State
Ohio Key[c]	4	1.8	2	Private

[a] Ranking is based on the following formula: 1 = ≥20 birds, or 15–19 birds and all three criteria met; 2 = 6–14 birds and two–three criteria met, or 15–19 birds and two criteria met.

[b] Criteria were: (1) habitat quality, i.e., excellent, with expansive mudflats adjacent to sandy beach; (2) historical data, i.e., presence on Christmas Bird Count at least once in previous five years; and (3) disturbance level, i.e., moderate to no disturbance at site (e.g., ≤1.4 people and/or 0.2 off-road vehicles observed per km).

[c] Ohio Key is an exception to the ranking system because it was the only location in the Florida Keys with consistent CBC data documenting Piping Plover use.

sites are under state/federal ownership. Sites that ranked a 3 or 4 were considered supporting sites, whereas sites ranked 5 probably are not quality sites and may represent incidental sightings (Nicholls 1989).

We recorded evidence of disturbance at 56% of the sites with no plovers, in contrast to 38% at sites with wintering plovers. We tallied an average of 3.5 people and 0.7 off-road vehicles per km at non-plover sites and 1.4 people and 0.2 off-road vehicles per km at plover sites. Plovers generally were seen foraging on sandflats near inlets, at tidal creeks, near dune ponds, and along the foreshore. Most roosting birds were found on the upper beach.

Gulf Coast survey.—The Gulf Coast survey covered 1283 km (739 km mainland and 739 km island) from the Everglades National Park, Florida,

to Brownsville, Texas. This included 176 sites comprising 50% of the total Gulf Coast; 39% actually were walked or driven (Table 1). Sites with potential habitat but not included in the survey were portions of the Big Bend Region and St. Joseph's Bay in Florida; Cat and Deer Islands in Mississippi; Breton National Wildlife Refuge (i.e., lower half of the Chandeleur Islands) and East and Central Isles Dernieres in Louisiana; and sections of the Laguna Madre in Texas and Mexico.

We counted 1508 Piping Plovers along the Gulf Coast from Florida to Texas (Table 2), which represented 35% of the total breeding population and 56% of the Great Lakes/Northern Great Plains population (Haig et al. 1988). Haig and Oring (1988b) reported only one Piping Plover breeding on the Atlantic Coast that was confirmed wintering along the Gulf Coast. Piping Plovers were observed most frequently in Alabama, Mississippi, Texas, and Louisiana (52–60% of the sites had birds) and least often in Florida (34% of the sites had birds) (Table 2). Louisiana (2.0/km) and Texas (1.6/km) had the highest Piping Plover density. Sites with the highest plover numbers were San Jose Island (N = 146) and Corpus Christi Pass (N = 108) in Texas, Chandeleur Islands (N = 80) in Louisiana, Bolivar Flats (N = 66) and Laguna Madre (N = 63) in Texas, Rockefeller Refuge (N = 52) in Louisiana, Honeymoon Island State Park (N = 53) in Florida, Little Dauphin Island (N = 50) in Alabama, Matagorda Peninsula (N = 50), Brazos Island State Park (N = 48), private land (i.e., between the Brazos and San Bernard Rivers in Brazoria County) (N = 48), Matagorda Island (N = 46) and San Bernard National Wildlife Refuge (N = 42) in Texas, and Mullet Key (N = 42) in Florida (Table 4). The other 61 sites had <40 birds per site; mean group size was 20.

On the Gulf Coast survey, we noted potential disturbances at 43% of the non-plover sites and 41% of the plover sites. Recreational activity also was higher at non-plover sites (6.5 people and 0.4 off-road vehicles per km) compared to plover sites (0.7 people and 0.2 off-road vehicles per km).

Piping plovers were found foraging on sandflats adjacent to passes and inlets, on mudflats near sandy beaches, on overwash sandy mudflats, and on the foreshore of open beaches (Nicholls 1989). Sites were ranked on the Gulf Coast using the same criteria described for the Atlantic Coast, excepting adjustments for the higher plover numbers, with 21 of the 27 most important sites under state/federal ownership (Table 4).

DISCUSSION

Atlantic Coast survey.—Georgia and South Carolina had the highest density of plovers per km surveyed and per km coastline, perhaps because both states contain numerous islands that create a diverse array of mi-

TABLE 4

IMPORTANT PIPING PLOVER WINTERING SITES ALONG THE GULF COAST, DECEMBER 1986–MARCH 1987

State Site	Plovers surveyed		Importance rank[a,b]	Ownership
	Number per site	Percent of survey total		
Florida				
Marco Island	18	1.2	2	Private
Estero Island	14	0.9	2	Private
Mullet Key	42	2.8	1	State
Honeymoon Island State Park	53	3.5	1	State
Sandbar Island[b]	17	1.1	2	State
Phipp's Reserve	25	1.7	2	Private
Cape San Blas	16	1.1	2	State
St. Joseph Peninsula	18	1.2	2	State
Crooked Island East	17	1.1	2	Federal
Shell Island	19	1.3	2	Federal
Alabama				
Little Dauphin Island	50	3.3	1	Federal
Mississippi				
Buccaneer State Park	10	0.7	2	State
Louisiana				
Chandeleur Islands	80	5.3	1	Federal
Isle Dernieres East	34	2.3	1	Private
Rockefeller Refuge	52	3.4	1	State
Texas				
Bolivar Flats	66	4.4	1	State
San Luis Pass	39	2.6	2	State
Private land[c]	48	3.2	1	Private
San Bernard NWR	42	2.8	1	Federal
Matagorda Peninsula	50	3.3	1	State
Matagorda Island	46	3.1	1	Federal
Corpus Christi Pass	108	7.2	1	State
San Jose Island	146	9.7	1	Private
Laguna Madre North	63	4.2	1	State
Laguna Madre South	29	1.9	2	State
South Padre Island	39	2.6	2	State
Brazos Island State Park	48	3.2	1	State

[a] Ranking based on the following formula and the same set of criteria used on the Atlantic Coast (see Table 3); 1 = >40 birds; 2 = 20–40 birds and 2–3 criteria met or 10–19 birds and three criteria met.

[b] Accreting sandbar between Honeymoon Island State Park and Anclote Keys NWR in Pinellas County.

[c] Land between the Brazos and San Bernard rivers in Brazoria County.

crohabitats (tidal inlets and creeks, barrier spits, tidal pools, and dune ponds) which may provide more plover habitat due to the heterogeneity of the coastline. Zivojnovich and Baldassarre (1987) speculated that habitat heterogeneity was an important factor influencing wintering Piping Plovers in Alabama, because multiple feeding and roosting sites occurred in close proximity. In contrast, long barrier islands and uniform stretches of beach characterize the North Carolina and Florida coasts. Therefore, reduced habitat diversity along these higher energy systems may explain lower plover numbers.

The CBC data from 1969–1984 were used to identify wintering sites of Piping Plovers (unpubl. data, C. Raithel, Rhode Island Dept. Environmental Management), and results of our survey generally were comparable. For example, CBC's for Virginia suggest that the species is a rare winter resident (e.g., only 52 Piping Plovers recorded from 1975–1985). Thus, the absence of Piping Plovers in Virginia during our survey indicates that North Carolina is the northern edge of the winter range on the Atlantic Coast. Similarly, Piping Plover sightings on CBC's along the Atlantic Coast of Florida are low. The CBC areas recognized by Raithel (unpublished data) as having a high frequency of Piping Plover occurrence (i.e., >10.0 plovers/100 person-h) also correlated with survey estimates. However, we identified the specific sites within CBC areas where Piping Plovers are actually found (see Nicholls 1989). For example, Piping Plovers tallied during the Morehead City CBC in North Carolina occur in the Rachel Carson's Estuary. Similarly, Piping Plovers reported on the Glynn County CBC in Georgia actually occur on Jekyll Island and Pelican Spit. Only a few CBC's such as Sapelo Island, Georgia, and Miami/Dade County, Florida, reported more birds than our survey, but local movements of birds, yearly fluctuations in habitat, or decline of the Atlantic Coast breeding population could explain survey differences at these sites.

Our survey also identified wintering areas never covered by CBC's, and thus unknown as concentration sites for wintering Piping Plovers. These sites include Portsmouth Island and Shackleford Banks in North Carolina; North and Little Capers Islands in South Carolina; Williamson, Ossabaw, Blackbeard National Wildlife Refuge, and Little St. Simon's Islands in Georgia; and Fort Mantanzas National Monument and Carl Ross Key in Florida.

Winter habitat loss is difficult to document, but historical data indicate that some degradation has occurred along portions of the Atlantic Coast (Dyer et al. 1987). For example, Piping Plovers were considered "abundant" from July to March in Florida (Stevenson 1960). Numerous man-made structures (e.g., seawalls, groins, and jetties) are present in Florida, and beaches typically are steep and narrow, reflecting severe erosion (U.S.

Department of Interior 1985). These factors may have reduced wintering plover habitat by eliminating feeding and roosting areas. Piping Plovers also spend a high percentage of time foraging during the winter period (Johnson and Baldassarre 1988), an activity that may be disrupted by frequent recreational activity. However, although our data suggest that human disturbance impacts wintering Piping Plovers on both coasts, because disturbance was less on sites with plovers versus sites without plovers, further research is needed to determine the exact mechanisms and degree of disturbance necessary to preclude use of an area by wintering Piping Plovers.

The Atlantic Coast survey located only 14% of the entire estimated Atlantic Coast population of Piping Plovers, yet we considered our survey coverage extensive (except in South Carolina) because it included 69% of the mainland and 58–85% of the offshore island barrier beach (Table 1). Clearly a large percentage of the population either is wintering in areas not surveyed or winters outside the United States.

A few anecdotal accounts indicate that Piping Plovers winter sporadically in the Bahamas and the Greater Antilles (Wetmore and Swales 1931, Bond 1947, Maurice 1953, Raffaele 1983), and Haig and Oring (1985) also reported sightings of wintering Piping Plovers in the Caribbean. From 1985–1988, two wintering Piping Plovers were sighted in the Greater Antilles, five in the Bahamas, one in Bermuda, one in Puerto Rico, one in the Virgin Islands, and one in Yucatan (Nicholls 1989). Group sizes of these sightings averaged 3.4, with the largest group (N = 15) reported from Eleuthera Island in the Bahamas in 1986. However, few coastal CBC's are conducted in the Caribbean, and birders rarely visit some islands, which may contribute to the paucity of sighting records. Thus, given that our survey coverage along the Atlantic Coast was extensive (69% of the total coastline) and that the average group size was only 6.0 plovers per site, there exists a strong possibility that wintering Piping Plovers are spread widely throughout the Caribbean islands. This dispersion may be beneficial, however, since small, scattered groups of plovers may be less vulnerable to climatic or man-made disasters than would be larger concentrations.

Gulf Coast survey.—On the Gulf Coast, Texas and Louisiana had the highest number of Piping Plovers per km surveyed. The barrier islands in these states are characterized by low-lying dunes and gently sloping beaches, which may offer more intertidal area for foraging shorebirds. The higher total plover count in Texas probably can be attributed to a longer barrier beach coastline, whereas Louisiana predominantly is fringed with coastal marsh. The Gulf side of Florida also contained a large percentage of the survey total, but the numbers per km surveyed and per km

of coastline were low. Perhaps the expansive sections of saltmarsh and mangrove reduce suitable habitat to more isolated patches. In contrast, the high density of Piping Plovers in Alabama may occur due to the diversity of habitats within the Mobile Bay barrier island system (Zivojnovich and Baldassarre 1987).

Raithel (1985, unpubl. data, Rhode Island Dept. of Environmental Management) identified historical concentration areas on the Gulf Coast, such as Port St. Joe in Florida, Dauphin Island in Alabama, and Bolivar Flats in Texas, which was supported by the 1984 survey of Haig and Oring (1985). Our survey results also corroborate these records (Nicholls 1989). However, increased coverage in Louisiana and Florida yielded additional wintering sites, such as the Chandeleur Islands, Fourchon Pass, Elmers Island, Isle Dernieres, Marsh Island, and Rockefeller Refuge in Louisiana, and Marco Island, Estero Island, Cayo Costa State Park, North Captiva Island, Anclote Keys, Hagen's Cove, Carabelle Beach, and Davis Point in Florida (these sites also are not included in CBC). Thus, given the previous surveys and that our survey accounted for approximately 56% of the entire Great Lakes/Northern Great Plains breeding population, the winter distribution of Piping Plovers on the Gulf Coast is becoming better known.

Deterioration of habitat used by wintering Piping Plovers has been suggested in portions of Alabama (Baldassarre 1986), Florida, and Texas (Haig et al. 1988). Hurricane Elena in 1985 was responsible for destroying intertidal flats used by plovers on the west end of Dauphin Island (Johnson 1987), however, increased development along the Alabama coastline also may have contributed to habitat loss. Future habitat loss may be imminent in Mississippi (beach restoration projects on mainland beaches), Louisiana (continuing coastal erosion), and Texas (new coastal development projects).

Total Gulf Coast coverage (50%) appears low because shoreline estimates include large sections of unsuitable habitat (e.g., saltmarsh) that were not surveyed. However, survey coverage of potential habitat (e.g., barrier beach) was more thorough. For example, coverage of the barrier beach coastline on the Gulf side of Florida was 78%, whereas total coastline coverage was only 44%. On the Gulf Coast, the highest potential for locating more plovers is in Louisiana, because only 27% of the barrier islands were covered. The lower Laguna Madre (below the Port Mansfield Ship Channel) in Texas also may yield more birds because of the expansive and relatively inaccessible sandflats and spoil islands throughout this system. Potential habitat also exists in the Laguna Madre de Tamaulipas (Tamaulipas), Altamira (Tamaulipas), and Rio Lagartos (Yucatan) (Haig and Oring 1985). Haig and Oring (1985) sighted few birds along the

Mexican Gulf Coast; however, only 25% of the coastline from Tamaulipas to the Yucatan peninsula was covered. Indeed, fluctuations of Piping Plover numbers during spring and fall migration along the Texas coast suggest that some birds may overwinter in Mexico (Blacklock and Rappole 1985).

CONCLUSIONS AND CONSERVATION RECOMMENDATIONS

Knowledge of winter distribution is of considerable importance in shorebird conservation (Myers 1983, Senner and Howe 1984, Morrison 1984) because such wide-ranging migrants often depend on several sites during their annual cycle (Morrison and Harrington 1979). Accordingly, the Western Hemispheric Shorebird Reserve Network has identified important staging and wintering areas for many shorebird species, and efforts have been made to protect these sites (Myers et al. 1987).

Conservation efforts for the Piping Plover also must include identification and protection of important wintering areas. Our survey documented exact locations of known Piping Plover wintering sites, and it also located previously unknown sites (see Nicholls 1989 for location maps). That 31 of the 39 sites we ranked as most important to Piping Plovers are under state/federal ownership indicates that protection efforts should focus on key winter habitats in private hands. We found that Piping Plovers usually occurred in small groups and were distributed unevenly along the two coasts. Sites with the largest concentrations of plovers generally consisted of expansive sandflats, or sandy mudflats, and sandy beach in close proximity. These diverse coastal systems, such as the barrier island complex of Mobile Bay or the Laguna Madre system in Texas, may concentrate wintering Piping Plovers because of the juxtaposition of roosting and feeding areas. Research efforts should determine the influence of habitat heterogeneity on the wintering ecology/distribution of the species.

Finally, coordinated regular censuses of major wintering sites could be effective in monitoring population status. An Atlantic Coast volunteer network was created to survey specific sites during 1987–1988 (Nicholls 1989). Results generally supported survey estimates and thus, if continued, may provide insight into yearly fluctuations and long-term site importance.

ACKNOWLEDGMENTS

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Zoology and Wildlife Science]). We thank all the Piping Plover Recovery Team members, especially leaders R. W. Dyer and S. M. Haig. The senior author is especially indebted to G. K. Stewart and M. J. Smar for their many hours of volunteer service in the field and for their friendship and patience. We also thank all those individuals who contributed to the project by offering logistical support and advice; their response was inspirational. The list of names would fill several pages and is an example of the outstanding dedication of many people to the conservation of Piping Plovers and other wildlife; we are grateful to all. This is publication no. 15-892204P of the Alabama Agricultural Experiment Station.

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NEST-SITE SELECTION BY EMPEROR GEESE AND CACKLING CANADA GEESE

MARGARET R. PETERSEN[1]

ABSTRACT.—Differences were found in habitat structure between nest sites of Emperor Geese (*Chen canagicus*) and Cackling Canada Geese (*Branta canadensis minima*) during a 5-year study (1982–1986) at Kokechik Bay, Alaska. Emperor Geese tended to select sites that afforded concealment from avian predators before incubation began. Cackling Canada Geese tended to select sites that enhanced avoidance of mammalian predators. Emperor Geese selected sites in areas away from open water, with tall dead vegetation adjacent to the nest site. Cackling Canada Geese selected sites close to shores of smaller ponds having more islands, and sometimes nested on islands, evidently enhancing avoidance of mammalian predators. During springs with heavy snow cover (>50% of surface covered on 25 May), both species selected sites appreciably different from sites selected during springs with light snow cover (<25% on 18 May). During heavy snow years, both species selected sites with more short, dead vegetation. Emperor Geese differed from Cackling Canada Geese by selecting sites with more shrubs and were farther from ponds. Cackling Canada Geese tended to nest closer together than Emperor Geese. Differences in structural habitat characteristics at nest sites of Cackling Canada Geese were not related to nesting success, but successful Emperor Geese selected nest sites with more and taller dead vegetation than unsuccessful pairs. Although it was possible to identify "typical" nest sites of Emperor Geese and Cackling Canada Geese, many sites were used by both species. Factors such as the amount and duration of snow cover, drainage patterns, presence or absence of islands, and type and abundance of egg predators play important roles in influencing nest-site selection and ultimately the distribution and abundance of Emperor Geese and Cackling Canada Geese. *Received 18 July 1989, accepted 15 Nov. 1989.*

Emperor Geese (*Chen canagicus*) and Cackling Canada Geese (*Branta canadensis minima*) nest primarily along the coastal fringe of the Yukon-Kuskokwim (Y-K) Delta, Alaska (Bellrose 1976). Geese nesting on the Y-K Delta received increased attention as their populations declined (O'Neill 1979, Petersen and Gill 1982, Raveling 1984, King and Derksen 1986, Pamplin 1986). The general nesting habitat and nest-site characteristics for these two species were described by Mickelson (1975) and Eisenhauer and Kirkpatrick (1977), but there have been no quantitative studies of nest sites of either species. Waterfowl nesting success of upland species may (e.g., Schranck 1972, Livezey 1981, Jackson et al. 1988) or may not (e.g., Glover 1956, Keith 1961, Dwernychuk and Boag 1972) be correlated with vegetative cover at nest sites, but the effect of cover at Emperor Goose and Cackling Canada Goose nests was unknown. My

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objectives were to: (1) evaluate structural features of nest sites of geese and to contrast those with features of sites not selected for nests, (2) evaluate the effect of snow conditions and the timing of nest initiation on structural features of nest sites, and (3) evaluate the relationship between features of nest sites and nesting success. These data are necessary to gain a more complete understanding of the influence of habitat and spring phenology on nesting distribution and success of nests of Emperor Geese and Cackling Canada Geese.

METHODS

Study area.—The 190-ha study area was at Kokechik Bay, 19 km NE of Hooper Bay, Alaska (63°39′N, 165°51′W). The flora, fauna, and physical features of the study area were described by Holmes and Black (1973), Eisenhauer and Kirkpatrick (1977), and Jackson (1981). The study area contains lowland, intermediate, and upland tundra similar to that described by Ely and Raveling (1984). Lowland tundra was less than 0.5 m above mean high tide and dominated by grasses and sedges; upland tundra was generally higher in elevation (to 1.5 m), and characterized by prostrate willows (*Salix* sp.), dwarf birch (*Betula nana*), and Labrador tea (*Ledum palustre*), and contained pingos similar to those described by Burns (1964); intermediate tundra contained plants characteristic of both upland and lowland tundra.

Data collection.—Measurements were obtained at each Emperor Goose and Cackling Canada Goose nest site and at a randomly determined site within 15 m of each nest immediately after the hatching period in early- to mid-July. Random sites were selected along a 30-m line running north and south through each nest site. The exact location was selected by using a random number table which included numbers 1 through 30. Random sites located in ponds or in standing water (marsh) were excluded, and new sites were randomly determined. Measurements of vegetation within a 1-m radius surrounding a nest or random site included (1) height of the tallest dead vegetation (±1.0 cm), (2) cover provided by dead vegetation surrounding the nest with a "Jones board" (Jones 1968) (i.e., vegetation present when the nest was initiated), and (3) proportions to the nearest 20% of tall vegetation (>0.5 m), short vegetation (<0.5 m), and shrubs. A score of 48 with the Jones board indicated no cover and 0 indicated complete cover. The proportions of tall and short vegetation and shrubs were estimated visually.

Measurements of physical features recorded for nests and random sites were: (1) distance (±0.1 m) to open water, (2) distance (±0.1 m) to marsh (standing water), (3) size (±1 ha) of the nearest pond, (4) number of islands in the nearest pond, (5) height (±1 cm) of the site above the water level of the nearest pond, (6) distance (±1 m) to the nearest nest of a conspecific, (7) distance (±1 m) to the nearest nest of the same species, and (8) when a site was on a pingo, the height (±1 cm) of the site below the top of the pingo. Distances greater than 50 m between goose nests and the sizes of ponds were measured from aerial photographs (1:5280 scale). The height of sites above normal pond water levels and below the tops of pingos were measured using a line level.

Nests were considered successful if one or more eggs hatched. Evidence of hatch included vocal or pipped eggs, goslings in the nest, or the presence of shell membranes from hatched eggs. Eleven Emperor Goose nests were excluded from the analysis of the characteristics of hatched and unsuccessful nests because I influenced their fates as part of another study.

Snow conditions.—Snow cover (%) on the study area in 1983–1986 was visually estimated from a four-m tall tower from the birds arrival to peak of nest initiation. In addition, oblique

photographs were taken each year from that same location on alternate days. Photographs taken in 1982 were matched to those dates in 1983–1986 with similar-appearing conditions and to the corresponding percentage of snow cover used for comparison between 1982 and other years.

Statistical analysis.—I used programs from SPSS^x (1986) to perform all statistical tests and to determine descriptive statistics. Most variables from random sites and nest sites had severely skewed distributions, and transformations to normalize the data (Sokal and Rohlf 1981) were ineffective. Because distributions of data within a variable were not always similar, I used Kolmogorov-Smirnov two-sample tests (Siegel 1956) to compare nest sites and random sites within species, nest sites between species, successful and unsuccessful nest sites within species, and nest sites used in heavy and light snow conditions between species. When appropriate, similar tests were used to compare random sites near Emperor Goose and Cackling Canada Goose nest sites. No significant differences were found ($P > 0.05$), thus all random sites were used when comparing random sites to nest sites. I used χ^2-tests (Sokal and Rohlf 1981) to evaluate the re-use of nest sites.

RESULTS

Comparison of nest sites and random sites.—Emperor Goose nest sites differed from random sites in one vegetative and four of six physical features (Table 1, Fig. 1). Emperor Goose nest sites had significantly larger amounts of shrubs near them than random sites ($Z = 4.8$, $P < 0.001$), were farther from open water ($Z = 1.85$, $P < 0.01$), were near ponds with fewer islands ($Z = 1.97$, $P < 0.001$), were higher above pond water levels ($Z = 4.8$, $P < 0.001$), and were positioned lower along the sides of pingos ($Z = 1.41$, $P < 0.05$). In contrast, nest sites of Cackling Canada Geese differed from random sites in three of five vegetative features (Table 1, Fig. 1); nest sites had shorter dead vegetation ($Z = 1.39$, $P < 0.05$), more short vegetation ($Z = 2.04$, $P < 0.001$), and less shrub ($Z = 1.71$, $P < 0.01$) than did random sites. Physical features were significantly different at random sites than at Cackling Canada Goose nest sites; nest sites were higher relative to pond water levels ($Z = 2.92$, $P < 0.001$), closer to open water ($Z = 4.50$, $P < 0.001$), farther from marsh areas ($Z = 2.22$, $P < 0.001$), closer to ponds with more islands ($Z = 3.15$, $P < 0.001$), and tended to be at smaller ponds ($Z = 1.70$, $P < 0.01$).

Interspecific differences in nest sites.—Nest sites selected by Emperor Geese and Cackling Canada Geese differed in three of five vegetative and five of six physical features (Table 1, Fig. 1). Emperor Geese selected nest sites that had taller dead vegetation ($Z = 1.68$, $P < 0.01$), less short vegetation ($Z = 2.34$, $P < 0.001$), and more shrub ($Z = 3.15$, $P < 0.001$). They were also farther from water ($Z = 2.86$, $P < 0.01$), closer to marsh areas ($Z = 2.43$, $P < 0.001$), near larger ponds ($Z = 2.37$, $P < 0.001$), near ponds with fewer islands ($Z = 4.5$, $P < 0.001$), and higher relative to pond water levels ($Z = 2.38$, $P < 0.001$) than nest sites selected by Cackling Canada Geese.

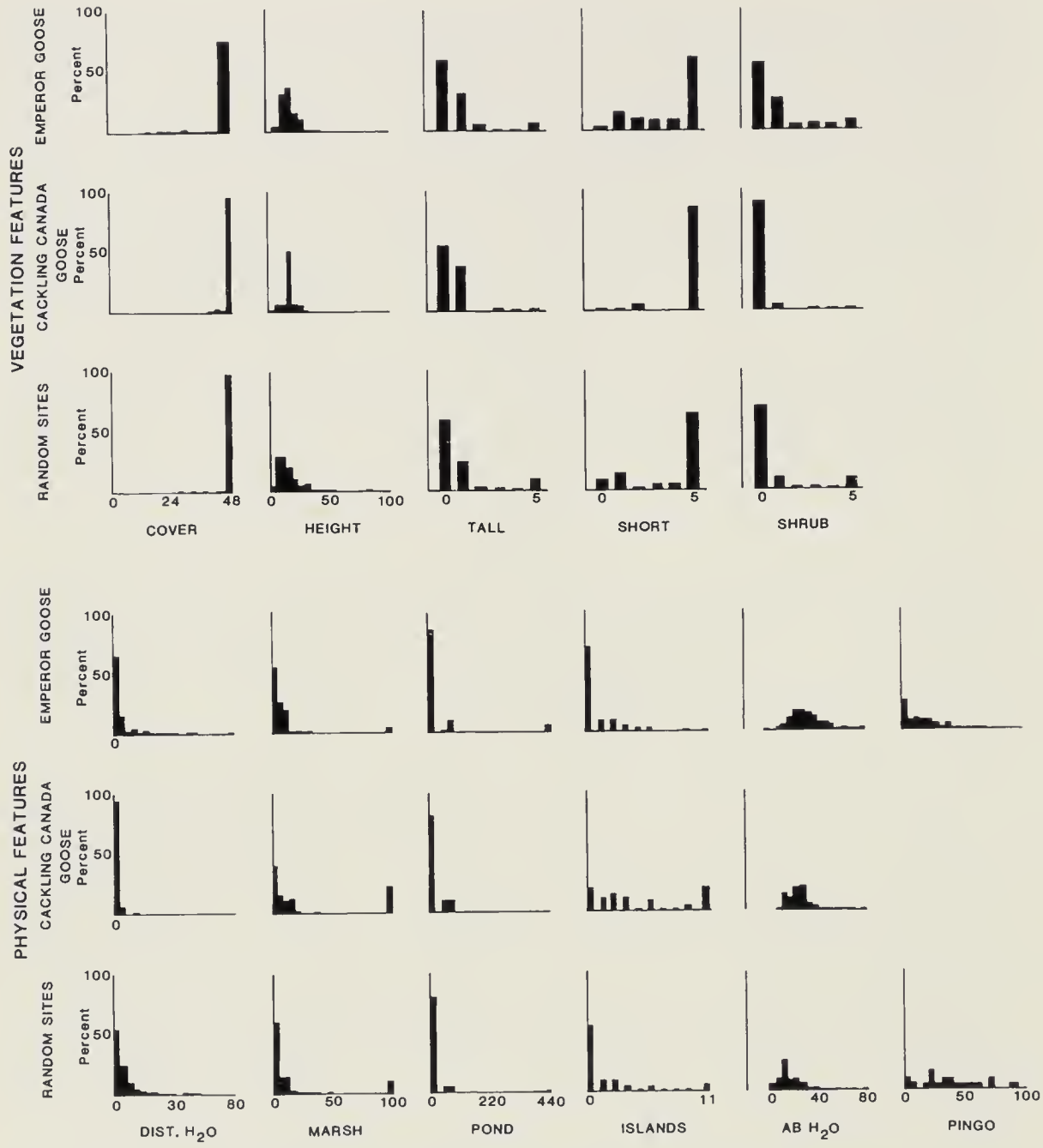

FIG. 1. Features of nest sites and random sites. Cover = cover score; height = height of dead vegetation (cm); tall = tall vegetation score; short = short vegetation score; shrub = shrub score; dist. H_2O = distance to open water (m); marsh = distance to marsh (m); pond = size of pond (ha); islands = number of islands in nearest pond; ab H_2O = height of site above pond water levels (cm); pingo = height of site below pingo top (cm).

Influence of snow conditions on nest-site selection.--Snow conditions on the study area varied among years and influenced timing of nest initiation (Fig. 2). Conditions in 1982, 1985, and 1986 were similar, with snow cover >75% on 18 May and still exceeding 50% on 25 May (heavy snow years). Snow conditions were similar in 1983 and 1984, with snow

TABLE 1

SIMILARITIES AND DIFFERENCES OF VARIABLE MEASUREMENTS BETWEEN RANDOM SITES AND NEST SITES

	Random sites	Emperor Goose nest sites	Cackling Canada Goose nest sites
Number of sites	300	197	117
Vegetative features			
Cover score	47.8 ± 0.10[a] (28–48)	46.4 ± 0.37 (16–48)	47.8 ± 0.10 (38–48)
Height of dead vegetation (cm)[b,c]	11.3 ± 0.52 (0–80)	11.4 ± 0.51 (0–45)	9.7 ± 0.63 (0–50)
Tall vegetation score (0–5)	0.9 ± 0.09 (0–5)	0.8 ± 0.09 (0–5)	0.7 ± 0.10 (0–5)
Short vegetation score (0–5)[a,b]	3.8 ± 0.11 (0–5)	3.8 ± 0.12 (0–5)	4.5 ± 0.12 (0–5)
Shrub score (0–5)[b,c,d]	0.8 ± 0.09 (0–5)	1.1 ± 0.11 (0–5)	0.2 ± 0.08 (0–5)
Physical features			
Distance to open water (m)[b,c]	4.67 ± 0.377 (0.1–42.6)	4.70 ± 0.580 (0.2–57.0)	1.29 ± 0.188 (0.2–13.6)
Distance to marsh (m)[b,c]	11.85 ± 1.263 (0.1–100)	8.68 ± 1.098 (0.5–100)	21.06 ± 2.628 (0.4–100)
Size of pond (ha)[b,c]	31.6 ± 4.97 (1–438)	39.8 ± 7.69 (1–438)	19.9 ± 2.49 (1–87)
Number of islands in nearest pond[b,c,d]	1.8 ± 0.17 (0–11)	0.7 ± 0.11 (0–11)	4.1 ± 0.38 (0–11)
Height of site above pond water levels (cm)[b,c,d]	19.4 ± 0.93 (−18–156)	32.1 ± 1.13 (−4–86)	25.5 ± 1.21 (8–90)
Height of site below pingo top (cm)[c,e]	34.5 ± 4.84 (0–86)	19.8 ± 3.23 (0–63)	9.0 ± 5.5 (3–20)
Distance to nearest goose nest (m)		88.0 ± 4.04 (13–317)	94.0 + 6.61 (9–529)
Distance to nearest goose nest of same species (m)		105.9 ± 5.00 (13–469)	123.8 ± 8.98 (9–642)

[a] All values are means ± one standard error; the range is in parentheses.
[b] Cackling Canada Goose nest sites significantly different from random.
[c] Emperor Goose nest sites significantly different from Cackling Canada Goose nest sites.
[d] Emperor Goose nest sites significantly different from random.
[e] Data from 24 random, 31 Emperor Goose nest, and 3 Cackling Canada Goose nest sites.

cover not exceeding 25% in May (light snow years) from the time of arrival of the geese through nest initiation. In heavy snow years, Emperor Geese selected nest sites that had shorter dead vegetation ($Z = 3.9$, $P < 0.001$), more shrubs ($Z = 2.56$, $P < 0.001$), and were farther from ponds

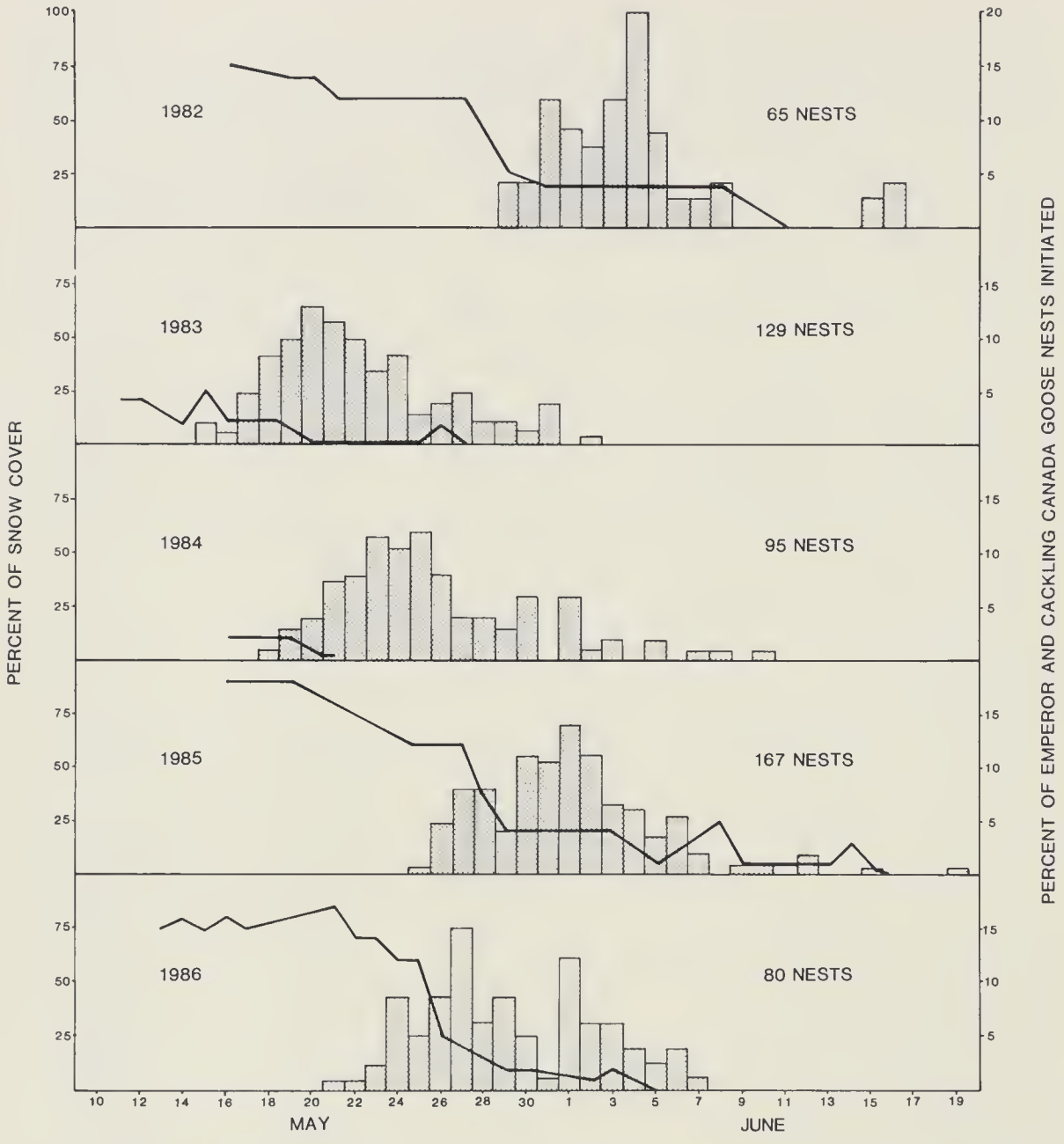

FIG. 2. Amount of snow cover (solid line) and proportions of nests (bars) initiated in each year from mid-May to early-June.

($Z = 1.94$, $P < 0.001$) than in light snow years (Fig. 3A). Nest sites selected by Cackling Canada Geese in heavy snow years had shorter dead vegetation ($Z = 2.16$, $P < 0.001$) and were closer to other Cackling Canada Goose nest sites ($Z = 1.37$, $P < 0.05$) than in light snow years (Fig. 3A).

Emperor Geese did not re-use nest sites, whereas Cackling Canada Geese frequently re-used nest sites. Re-use of nest sites by Cackling Canada Geese appeared to be related to snow conditions; re-use of old nest sites was more frequent (42.9% of 156) in years with heavy snow con-

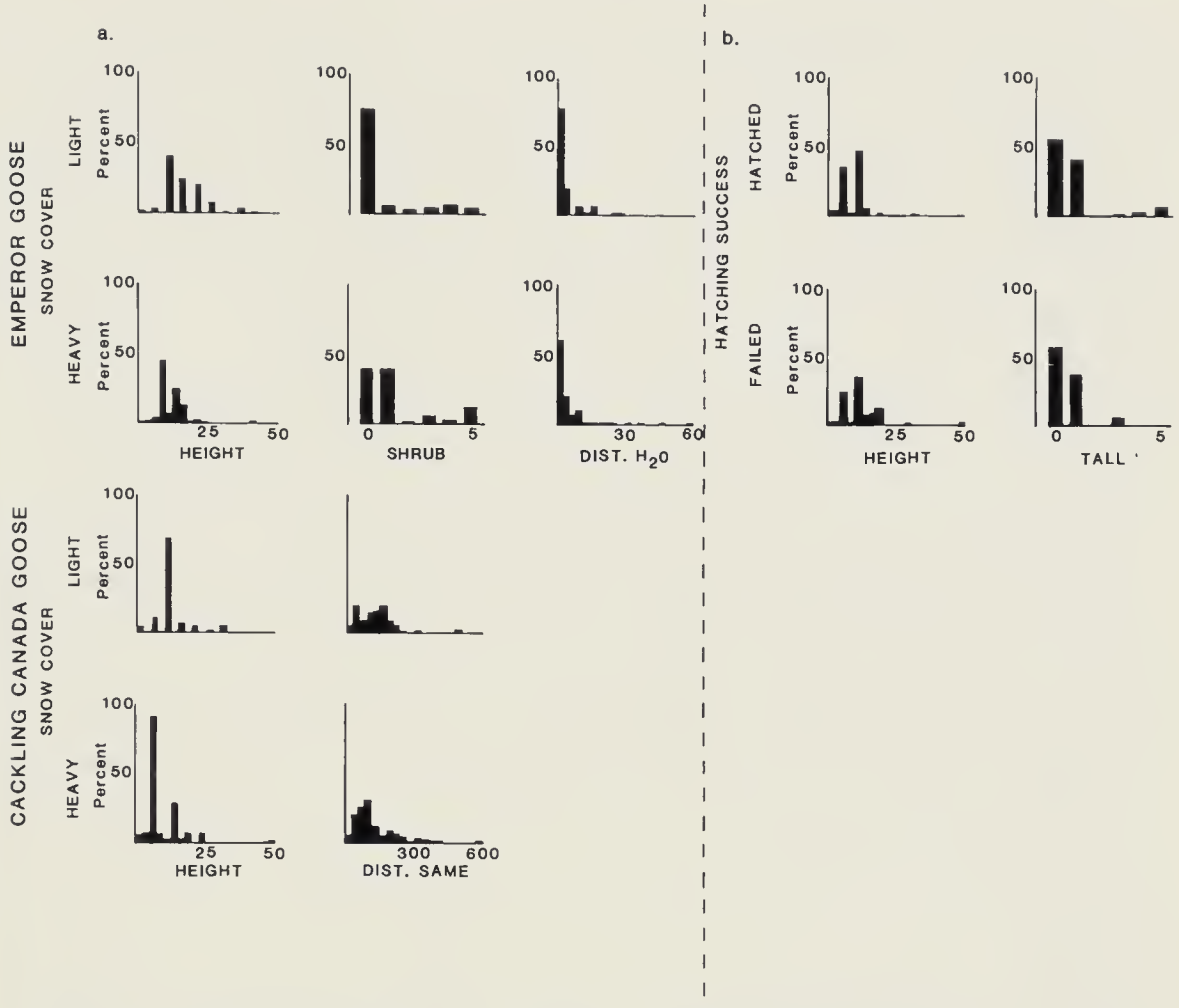

FIG. 3. Proportions of each value for each variable significantly different ($P < 0.05$) at nests (A) during heavy and light snow conditions and (B) at successful and unsuccessful nest sites. Captions on graphs the same as Fig. 1 except dist. same = distance to nearest goose nest of the same species (m).

ditions than in years (19.4% of 98) with light snow conditions ($\chi^2 = 15.0$, df = 1, $P < 0.005$).

Nest-site selection and time of nest initiation.—In springs with heavy snow cover, the earliest-nesting Emperor Geese selected more elevated nest sites relative to pond water levels (Fig. 4). As the season progressed and other sites became available (through the thawing and drying of those sites), Emperor Geese selected lower nest sites. This trend was suggested but not significant in years with light snow cover. Cackling Canada Geese selected sites that were higher above pond water levels early in the season and selected lower sites later in the spring in both heavy and light snow seasons (Fig. 4).

Characteristics of successful and unsuccessful nest sites.—Successful nest sites of Emperor Goose differed significantly from unsuccessful nest sites

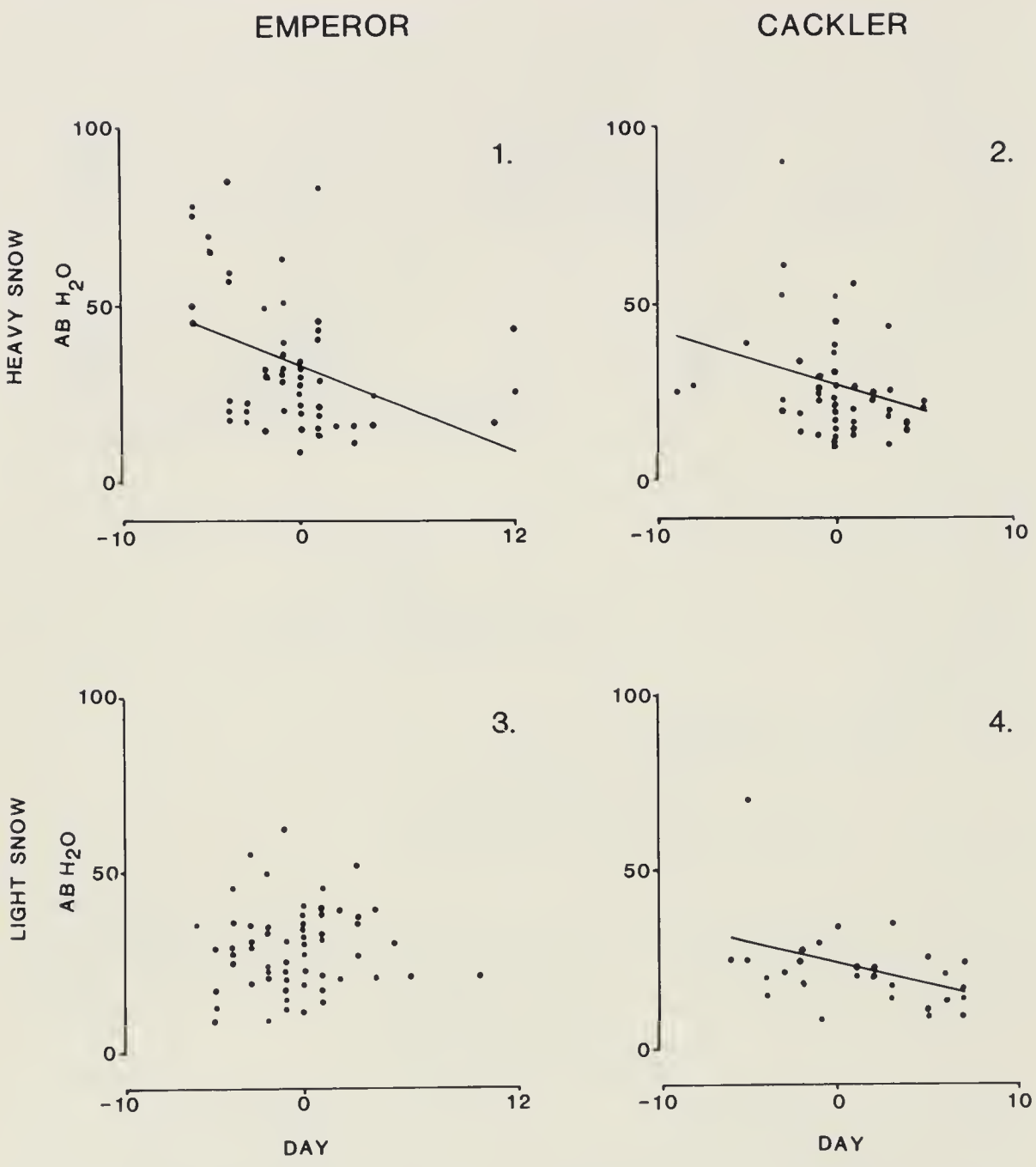

FIG. 4. Relation between date of nest initiation for Emperor Geese and Cackling Canada Geese and height of the nest above pond water levels in years with heavy and light snow cover. 0 represents the model initiation date. Statistics are as follows: 1. N = 58, $r = -0.369$, $P < 0.005$; 2. N = 51, $r = -0.280$, $P < 0.055$; 3. N = 63, $r = 0.060$, $P > 0.10$; 4. N = 31, $r = -0.391$, $P < 0.01$.

by the height of the dead vegetation ($Z = 1.40$, $P < 0.05$) and by having more tall vegetation ($Z = 1.58$, $P < 0.05$) (Fig. 3B). Successful and unsuccessful nests of Cackling Canada Geese had similar vegetative and physical features.

DISCUSSION

Habitat features.—Nest sites used by either Emperor Geese or Cackling Canada Geese were not distinguishable by vegetative cover when compared to random sites. Sites available to geese in the general area rarely contained sufficient tall, dense grasses, sedges, or shrubs to provide complete cover to conceal such a large bird (Fig. 5 above). Emperor Geese selected sites with more shrubs than did Cackling Canada Geese or that were found at random sites, but shrubs rarely provided concealment of the nest. Shrubs were generally the understory to grasses and sedges (Fig. 5 below) and only along the sides of some pingos in upland habitat were shrubs tall enough to provide cover to nests. These sites were infrequently used; only 17% of Emperor Goose nests and 3% of Cackling Canada Goose nests were located on pingo sides. Cackling Canada Geese tended to select sites with more shorter, dead vegetation than random sites, although much of the vegetation was too short to provide concealment from mammalian or avian predators. This observation is consistent with studies of larger subspecies of nesting Canada Geese that suggest that geese select nest sites with less vegetation, enhancing visibility by geese (e.g., Sherwood 1968, Kaminski and Prince 1977), and with Mickelson (1975) who suggested that Cackling Canada Geese avoid areas with tall, dead grass which reduces visibility. Emperor Geese did not use sites with significantly taller, dead vegetation than available at random sites. This is in contrast to Mickelson's (1975) conclusions that Emperor Geese use sites with tall vegetation. It seems that both Emperor Geese and Cackling Canada Geese select nest sites which are not concealed and that have good visibility.

The physical feature that appears to be the most influential in nest site selection for both species and in the timing of nest initiation is the height of the nest site above pond water levels. The data presented here supports the suggestions of Eisenhauer and Kirkpatrick (1977), Mickelson (1975), and Dau and Mickelson (1979) that nests initiated early are at higher locations than nests initiated later in a season, a pattern that was particularly evident here in springs with heavy snow cover. Accordingly, it seems likely that nest-site selection by Emperor Geese and Cackling Canada Geese is dependent on snow-free, dry locations.

If height of the site alone were a key aspect in nest-site selection, then sites on top of pingos should have been favored. This selection did not occur; geese that did nest on pingos selected the sides rather than the tops of these mounds. A factor limiting the availability of such nest sites could be the depth of soil that is thawed when a female goose investigates a site and attempts to dig a nest scrape. Burns (1964) found that soils with little litter accumulation (grass covered) had thawed more than soils with great-

FIG. 5. Typical nest site of Emperor Geese showing: (above) the lack of abundant tall vegetation for nest concealment and (below) shrubs as an understory to short vegetation.

er litter accumulation (heath atop pingos). Depth of thawed soil (or soil temperature) may possibly be an important factor in nest-site selection, and perhaps the timing of nest initiation, by Emperor Geese and Cackling Canada Geese.

Emperor Geese and Cackling Canada Geese selected substantially different nest sites. This observation is not unexpected, because Cackling Canada Geese are about two-thirds the size of Emperor Geese (Palmer 1976) and have evolved different anti-predator nesting strategies (Mickelson 1975, Thompson and Raveling 1987). However, I was unable to detect differences in features of the nest habitat which reliably separate the two species. Distributions of the values of the various features overlapped, and a few (N = 10) Cackling Canada Geese used nest sites that were used by Emperor Geese in previous years.

Effect of snow cover on nest-site selection.—Although the amount of snow cover had a measurable effect on habitat features of nest sites, the primary differences between years were the greater proportion of nests re-used by Cackling Canada Geese when snow cover was most extensive and differences in timing of nest initiation by both species. Underlying factors may include the availability of suitable nest sites and the proportion of older, more experienced geese that nest in years with heavy snow cover (late years). Sites available to Lesser Snow Geese (*Chen caerulescens caerulescens*) for nesting were restricted in some years because of heavy snow cover (Cooke and Abraham 1980), and during such late seasons a smaller proportion of young Lesser Snow Geese nest (Finney and Cooke 1978). It is also possible that fewer young Cackling Canada Geese may nest in late seasons with heavy snow cover. Individually marked Cackling Canada Geese used the same nest sites in successive years (Mickelson 1975, Petersen, unpubl. data). Thus the higher proportion of re-used nest sites in heavy snow conditions may represent a higher proportion of older, more experienced geese.

Habitat features associated with nesting success.—Successful Emperor Geese appear to select nest sites that provide at least minimal concealment from predators. Emperor Geese successfully defend their nests against arctic foxes (*Alopex lagopus*) (R. M. Anthony, pers. comm., Petersen, unpubl. data), and losses of eggs to foxes in most areas was comparatively low (Mickelson 1975, Eisenhauer and Kirkpatrick 1977). Fox predation on the Kokechik Bay study area in 1982–1986 was higher than that reported by Mickelson (1975) or Eisenhauer and Kirkpatrick (1977), with most of the losses of eggs occurring during three of the five seasons. In those years, foxes tended to remove eggs from all nests within an area. For example, in 1986 only 7 of 58 (12.1%) nests in a 190-ha area had one or more eggs hatch; an adjacent 227-ha area of similar habitat had

56 of 88 (63.6%) nests successful. Evidently, features of the habitat did not influence predation by arctic foxes during those seasons.

Losses to avian predators, primarily Parasitic Jaegers (*Stercorarius parasiticus*) and Glaucous Gulls (*Larus hyperboreus*), are the primary causes of egg mortality of Emperor Geese (Mickelson 1975, Eisenhauer and Kirkpatrick 1977). From the first until the penultimate egg, Emperor Geese are infrequently at the nest (Petersen, unpubl. data) and, when they leave, conceal the eggs and nest with vegetation from the immediate vicinity (Eisenhauer and Kirkpatrick 1977, Krechmar and Kondratiev 1982). During this 5–7-day period prior to incubation nests are susceptible to avian and mammalian predators, and the presence of tall grasses at the nest may provide additional material necessary to conceal the eggs and nest. After the clutch is complete, losses of eggs to avian predators are apparently diminished by almost constant incubation by the geese (Thompson and Raveling 1987). Thus the selection of nest sites with tall, dead grasses may be in response to avian and mammalian predation early in the nesting period.

None of the habitat features I measured was important for identifying successful and unsuccessful Cackling Canada Geese nests. Other studies (Mickelson 1975, Thompson and Raveling 1987, Petersen unpubl. data) showed that Cackling Canada Geese that nest on islands are more successful than those nesting on shorelines or on islands that have been connected to shore, presumably because foxes are reluctant to swim to islands. The physical and vegetative features that I measured were similar for random sites at all locations; the features of each nest site were similar regardless of the location. Apparently, the features immediately surrounding the nest sites of Cackling Canada Geese do not influence their success. The selection of a particular island and the timing of nest initiation within a year is strongly influenced by snow melt and drainage patterns of ponds, whereas the tendency to use islands that are suitable for nest sites is strongly influenced by lower predation rates of nests on islands.

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AVIAN COMMUNITY RESPONSES TO HYDRILLA INVASION

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ABSTRACT.—Changes in a bird community associated with increased coverage of the exotic submergent hydrilla (*Hydrilla verticillata*) were studied on a Texas reservoir. Hydrilla was the only major plant exhibiting a significant increase in areal coverage from 1986 to 1987. Bird species richness and total bird numbers in 1987 correspond to increased hydrilla coverage, as well as substantial increases in populations of birds shown to be closely associated with hydrilla, e.g., American Coots (*Fulica americana*), Pied-billed Grebes (*Podilymbus podiceps*), and several duck species. Observations of sample plots demonstrated a correlation between hydrilla coverage and bird use, especially for American Coots. Experimental removal of hydrilla from plots resulted in a decrease of bird use of plots lacking hydrilla. The addition of the submergent layer of hydrilla was beneficial to the bird community, presumably due to increased horizontal vegetative diversity and foraging opportunities. *Received 12 April 1989, accepted 6 Nov. 1989.*

Vegetation influences bird community structure, i.e., bird numbers and diversity. Most studies of such relationships have considered terrestrial systems, concentrating either on the role of vertical (MacArthur and MacArthur 1961, MacArthur et al. 1962, Karr and Roth 1971, Willson 1974, and many others) or horizontal structure (Wiens 1974, Roth 1976, Rotenberry and Wiens 1980, Rice et al. 1984). The relationship between wetland bird communities and habitat diversity has been addressed for nesting birds and emergent vegetation (Weller and Spatcher 1965, Weller 1979, Weller and Voigts 1983, Burger 1985). The present paper focuses on the dynamics of the wetland bird community during the early stages of the invasion of the submergent hydrilla (*Hydrilla verticillata*) in a Texas reservoir. Using both experimental and observational methods, the role of hydrilla as an influencing factor on bird numbers and species richness was addressed.

Hydrilla, an exotic submerged macrophyte, was first reported in the United States from Florida in 1960 (Blackburn and Weldon 1969) and has spread to at least 12 other states (Johnson and Montalbano 1987). Once established, hydrilla often dominates water bodies and causes significant changes in vegetation structure (Haller and Sutton 1975). This dramatic habitat change also influences other components of lake systems. Aquatic macroinvertebrate abundance and richness generally increase with the addition of submergents (Krull 1970), as is the case with hydrilla

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(Moxley and Langford 1982, Watkins et al. 1983). Forage fish production also increases with the initial hydrilla invasion (Moxley and Langford 1982). These system changes would be expected to influence abundance of birds utilizing fish and invertebrate resources.

The relationship between birds and hydrilla has been described in a number of Florida studies. Hydrilla was an important food for American Coots (*Fulica americana*) (Montalbano et al. 1979, Hardin et al. 1984), Common Moorhens (*Gallinula chloropus*) (Mulholland and Percival 1982, O'Meara et al. 1982), and several duck species (Montalbano et al. 1978, 1979; Hardin et al. 1984). Hydrilla also has been shown to be a highly utilized habitat component by Florida waterfowl. Reductions in waterfowl abundance were observed following hydrilla removal by grass carp (*Ctenopharyngodon idella*) (Gasaway and Drda 1977). Hydrilla was highly used by waterfowl on Lake Okeechobee and supported a greater diversity of duck species than other plant communities (Johnson and Montalbano 1984). This study serves to further describe bird-hydrilla relationships in a reservoir outside of Florida, and for a wide range of birds, providing the first assessment of associated community change.

STUDY AREA AND METHODS

Lake Fairfield is located 18 km east of Fairfield in Freestone County, Texas. Dam construction was completed in 1969, and the lake reached mean pool level of 94.5 m above sea level in 1971. Hydrilla was first observed in Lake Fairfield in 1984 (Durocher 1986, K. Strawn, pers. comm.), and this study was initiated in 1986. Mean water depth is 6.5 m and annual water fluctuation less than 1 m. The main body of the lake encompasses 1053 ha with an adjacent 60-ha cooling pond and 3.3 km of canals. Recreational use includes fishing, boating, and water skiing, but no hunting is permitted on the lake or in adjacent areas. Upland vegetation surrounding the lake is typical of the post oak savannah region of Texas (Gould 1962).

Vegetation sampling.—Vegetation of the lake was surveyed every three months from summer 1986 through fall 1987. Seasons were defined by equinoxes and solstices, and vegetation surveys were conducted at mid-season. Twenty-three 50 × 50 m plots were located throughout the lake and marked with survey flagging and buoys. Three plots were randomly located in open water areas where variance was zero due to lack of any vegetation. The remaining 20 plots were randomly placed adjacent to shore, encompassing the band where all aquatic vegetation was located. Plots on shore were sampled using line transects. Three randomly located, 50-m lines perpendicular to shore were established within each shoreline plot. Beginning at the shoreward edge above the high water mark, plant species present directly above or below a point at each 0.5 m along each line were recorded. Results from the 20 plots adjacent to shore were extrapolated to represent the vegetated portion (227.4 ha) of the lake which was within 50 m of shore, and open water plot results represented the 825.6 ha of the lake which was more than 50 m from shore. Friedman's two-way analysis of variance (ANOVA) (Conover 1980:299–308) was used to detect changes in abundance of a single plant species or habitat type over the six seasons of vegetation sampling. In this case, and in all other instances in which Friedman's test is used, the F approximation was used rather than the Chi-squared approximation due to increased test efficiency (Conover

1980:300). A Fisher's Least Significant Difference (LSD) multiple comparisons procedure (Ott 1984:365–370) was used to separate seasons differing in abundance.

Abundance of all habitat types over all seasons combined was compared using Friedman's two-way ANOVA. Fisher's LSD was used to determine where differences in habitat abundance lay.

Bird surveys.—The avifauna of Lake Fairfield was surveyed by boat to determine species richness and population sizes. Surveys were conducted semimonthly during fall, winter, and spring, weekly during summer 1986, and monthly during summer 1987. Forty-eight total surveys were completed; 28 in 1986 and 20 in 1987. Surveys were conducted soon after sunrise and on weekdays, when possible, to avoid weekend boat disturbance. Duration of surveys ranged from three to six hours and direction around the lake was alternated.

Bird species richness was compared across habitats for each season using a one-way ANOVA followed by Fisher's LSD post-test to determine interhabitat differences. This assessment was designed to determine the relative value of each habitat throughout the seasons and was conducted both for all birds and for ducks.

Bird survey data were used to compare community structure parameters across seasons using a one-way ANOVA with a Fisher's LSD post-test. This procedure allowed for the detection of changes in community structure parameters through the seasons and across years for individual species, groups of species, and for the bird community as a whole. Species diversity indices were not used as measures of community structure due to questionable use and interpretation (Hurlbert 1971, James and Rathbun 1981).

Bird observation plots.—Plot observations were conducted to assess the relationship between vegetation and bird use. Plots were the same as those used for vegetation analyses and were observed on each of seven dates throughout winter and fall 1987. Plots were observed from a boat for a period of 10 min, during which time bird species and number of individuals present were noted. Using data collected from plot observations, coefficients of linear correlations (Neter et al. 1985:96–99) were calculated to determine if there was a significant correlation between bird use and the amount of hydrilla across plots.

Experimental plots.—Four hydrilla-free plots were created in August 1986 within hydrilla beds to further assess the importance of hydrilla to certain bird species and assemblages. Hydrilla-free plots were created with the herbicide Aquathol K (Pennwalt Corp., 3 Parkway, Philadelphia, PA 19102), and the openings were maintained by manual removal as necessary through fall 1986 and winter 1987. The cleared plots were 50 × 50 m and each was located near one of the bird observation plots which showed an abundance of hydrilla. The experimental plots and adjacent hydrilla plots were observed on seven dates in fall 1986, six dates in winter 1987, and five dates in spring 1987 in the same manner as described for the plot observations.

Experimental plots lacking hydrilla and corresponding hydrilla plots were compared using the Wilcoxon signed-rank paired comparison (Conover 1980:280–288) to determine if there was a difference in bird use between the two treatments. This was done for the entire bird community and selected groups and species of birds.

RESULTS

Vegetation of Lake Fairfield was grouped into nine habitat types: hydrilla, emergents, emergent-hydrilla interface, submergents other than hydrilla, floating-leaf plants, nonpersistent emergents, terrestrial vegetation, unvegetated shoreline/shallow water, and open water. Coverage of each habitat type by season is presented in Table 1. Significant differences

TABLE 1

SEASONAL HABITAT COVERAGE IN HECTARES AT LAKE FAIRFIELD, TEXAS (1986–1987)

Habitat	1986			1987		
	Summer	Fall	Winter	Spring	Summer	Fall
Open water	954.6 (90.66)[a]	944.9 (89.73)	993.4 (94.34)	983.6 (93.41)	929.7 (88.29)	911.9 (86.60)
Hydrilla	29.2 (2.77)	41.1 (3.90)	19.9 (1.89)	10.4 (0.99)	44.1 (4.19)	53.2 (5.05)
Emergent	22.6 (2.15)	24.9 (2.36)	25.5 (2.42)	26.6 (2.53)	24.7 (2.35)	23.3 (2.21)
Floating leaf	21.1 (2.00)	17.2 (1.63)	0.0 (0.00)	15.6 (1.48)	25.1 (2.38)	14.8 (1.41)
Unveg. shore shallow water	8.6 (0.82)	15.4 (1.46)	10.6 (1.01)	10.7 (1.02)	10.0 (0.95)	25.0 (2.37)
Other submergents	9.0 (0.85)	5.5 (0.52)	0.3 (0.03)	2.0 (0.19)	10.1 (0.96)	10.8 (1.03)
Terrestrial vegetation	0.5 (0.05)	0.1 (0.01)	1.9 (0.18)	1.8 (0.17)	5.3 (0.50)	6.6 (0.63)
Emergent-hydrilla	5.9 (0.56)	2.9 (0.28)	1.3 (0.12)	1.1 (0.10)	3.8 (0.36)	4.6 (0.44)
Nonpersist. emergent	1.5 (0.14)	0.9 (0.09)	0.0 (0.00)	1.2 (0.11)	0.1 (0.01)	2.6 (0.25)

[a] Percent coverage is in parentheses.

($F = 24.59$, $P < 0.001$) in coverage were found across habitats. Open water was more abundant than all other habitat types. Hydrilla and emergent habitat types were more abundant than the remaining habitat types. Floating-leaf, unvegetated shoreline/shallow water, and other submergent habitat types were more abundant than terrestrial vegetation, emergent-hydrilla interface, and nonpersistent emergent habitats.

Hydrilla was the only common habitat type to increase significantly ($P < 0.05$) across years. An increase in areal coverage of hydrilla of 51% was observed from summer 1986 to summer 1987 and an increase of 33% was noted across corresponding falls. The other submergent habitat type, which consisted primarily of spiny naiad (*Najas marina*), also increased across years. However, its influence on the bird community was minimal because it was uncommon and received very little bird use. Nonpersistent emergent and terrestrial vegetation habitats exhibited increases across years; however, these uncommon habitats also received little bird use. Open water coverage decreased across years, corresponding to invading hydrilla.

Avian species richness was compared across the six major habitats to determine the relative value of each habitat (Table 2). Unvegetated shoreline/shallow water habitat averaged the most species per survey with open water being second, although the two did not differ statistically. Hydrilla ranked fourth and had more species than floating-leaf and emergent-hydrilla interface habitats. Hydrilla was ranked first in species richness for fall 1987 and second, although not significantly less rich than the top-ranked open water habitat, for fall 1986 and winter 1987.

Comparisons of species richness across habitats also were calculated for ducks only (Table 3). In summer 1986, only Wood Ducks (*Aix sponsa*), found almost exclusively in American lotus, were present. Hydrilla supported the greatest duck species richness in the falls of both years and winter 1987, the seasons of greatest duck abundance. Johnson and Montalbano (1984) found similar results in Florida, where hydrilla attracted a greater diversity of waterfowl species than several other habitats.

Plot observations indicated a significant ($P < 0.001$) correlation between bird numbers and the amount of hydrilla in plots for winter and fall 1987 and also for these seasons combined ($R^2 = 0.541$). American Coots constituted most of the bird use of the plots in these seasons and the strength of the correlation between number of individuals and hydrilla amount for coots is similar ($R^2 = 0.520$). Coots were the only species observed in the plots in sufficient abundance to independently support analysis.

Experimental plots also served to elucidate the relationship between birds and hydrilla. The coverage of hydrilla in the plots of both treatments was similar in summer 1986 before herbicide application and manual removal of hydrilla from experimental plots (Fig. 1). However, in the following fall and winter, hydrilla coverage in experimental plots was significantly less than that in hydrilla plots. By spring 1987, the plots of both treatments again had similar hydrilla coverage. Fall 1986 and winter 1987 seasons provided the best comparisons of differential bird use between treatments because they had the greatest difference in hydrilla amounts and, also, were the seasons with greatest bird abundance.

Total bird use was substantially lower in plots without hydrilla for fall 1986 ($P = 0.0062$) and winter 1987 ($P = 0.0007$) (Fig. 2); however, total bird use was similar between treatments for spring 1987, the season for which hydrilla amounts also were similar (Fig. 1). American Coots constituted a large portion of the total bird use for both treatments, reflecting the relative abundance of this species, and were much more numerous in hydrilla plots. The difference in coot numbers between treatments was significant in fall 1986 ($P = 0.0062$) and in winter 1987 ($P = 0.0002$). Pied-billed Grebes (*Podilymbus podiceps*) also demonstrated a significant

TABLE 2

MEAN BIRD SPECIES RICHNESS ACROSS SEASONS AND MAJOR HABITATS ON LAKE FAIRFIELD, TEXAS (1986–1987). WITHIN SEASONS, HABITATS SHARING A LETTER DID NOT DIFFER ($P > 0.05$)

Season	Habitat					
	HYD	EMG	E/H	FLT	USS	OPN
Summer 1986	2.182 (E)	5.636 (AB)	2.364 (DE)	4.455 (BC)	7.000 (A)	3.727 (CD)
Fall 1986	6.833 (AB)	3.167 (C)	3.000 (C)	2.500 (C)	5.667 (B)	7.667 (A)
Winter 1987	7.200 (AB)	6.200 (B)	2.400 (C)	1.400 (C)	6.400 (B)	9.800 (A)
Spring 1987	3.333 (CD)	8.500 (AB)	1.833 (D)	1.500 (D)	11.000 (A)	5.833 (BC)
Summer 1987[b]	5.000	4.333	2.000	3.000	3.000	3.667
Fall 1987	13.167 (A)	5.000 (BC)	2.167 (C)	3.000 (C)	7.500 (B)	11.333 (A)
Overall	5.116 (C)	5.860 (BC)	2.000 (D)	2.767 (D)	7.349 (A)	6.698 (AB)

[a] Habitat abbreviations: HYD = hydrilla; EMG = emergent; E/H = emergent-hydrilla interface; FLT = floating leaf; USS = unvegetated shoreline/shallow water; OPN = open water.
[b] Habitats were not different ($P = 0.1018$).

TABLE 3

MEAN WATERFOWL SPECIES RICHNESS ACROSS SEASONS AND MAJOR HABITATS AT LAKE FAIRFIELD, TEXAS (1986–1987). WITHIN SEASONS, HABITATS SHARING A LETTER DID NOT DIFFER ($P > 0.05$)

Season	Habitat[a]					
	HYD	EMG	E/H	FLT	USS	OPN
Summer 1986	0.091 (B)	0.000 (B)	0.000 (B)	0.636 (A)	0.000 (B)	0.00 (B)
Fall 1986	2.167 (A)	0.000 (B)	0.167 (B)	0.333 (B)	0.167 (B)	0.833 (B)
Winter 1987	2.400 (A)	0.800 (B)	0.000 (B)	0.600 (B)	0.200 (B)	1.200 (AB)
Fall 1987	5.833 (A)	0.333 (B)	0.167 (B)	1.333 (B)	0.167 (B)	1.167 (B)
Overall	1.500 (A)	0.386 (BC)	0.045 (C)	0.500 (BC)	0.318 (BC)	0.545 (B)

[a] Habitat abbreviations are the same as those in Table 2.

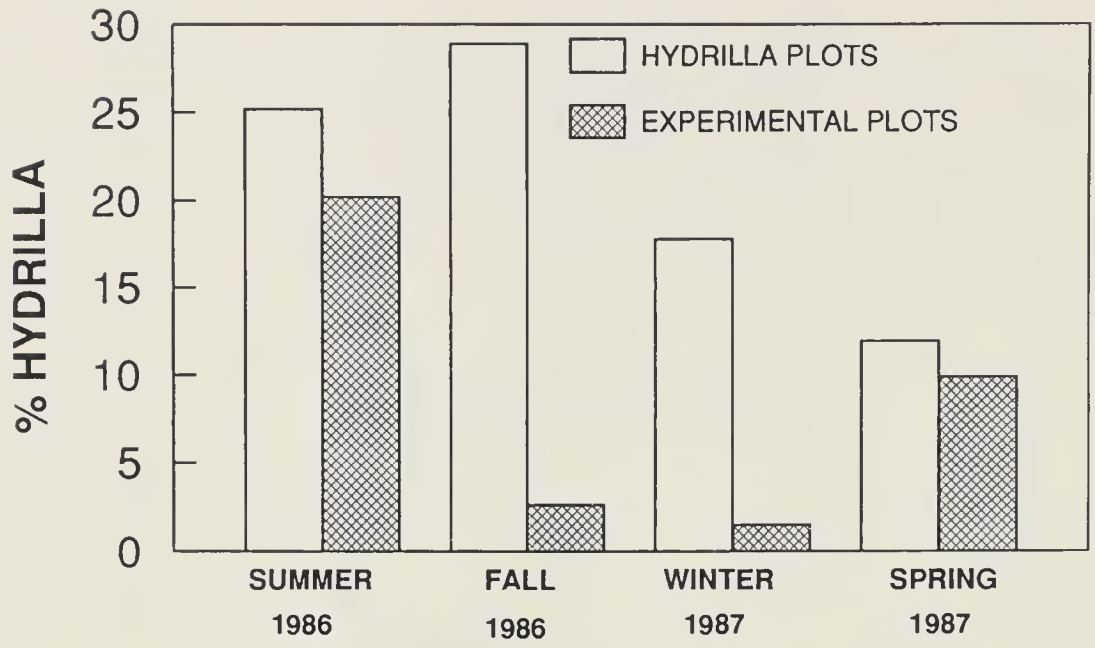

FIG. 1. Percent hydrilla coverage in hydrilla and experimental plots, Lake Fairfield, Texas, 1986–1987. Herbicide was applied to experimental plots between summer and fall 1986.

($P = 0.0312$) preference for hydrilla plots in fall 1986 but not in the following winter ($P = 0.5332$).

Changes in bird community structure reflected typical seasonal differences in taxa and bird numbers and yearly differences due to habitat changes. Species richness differed ($F = 5.75$, $P < 0.001$) across seasons

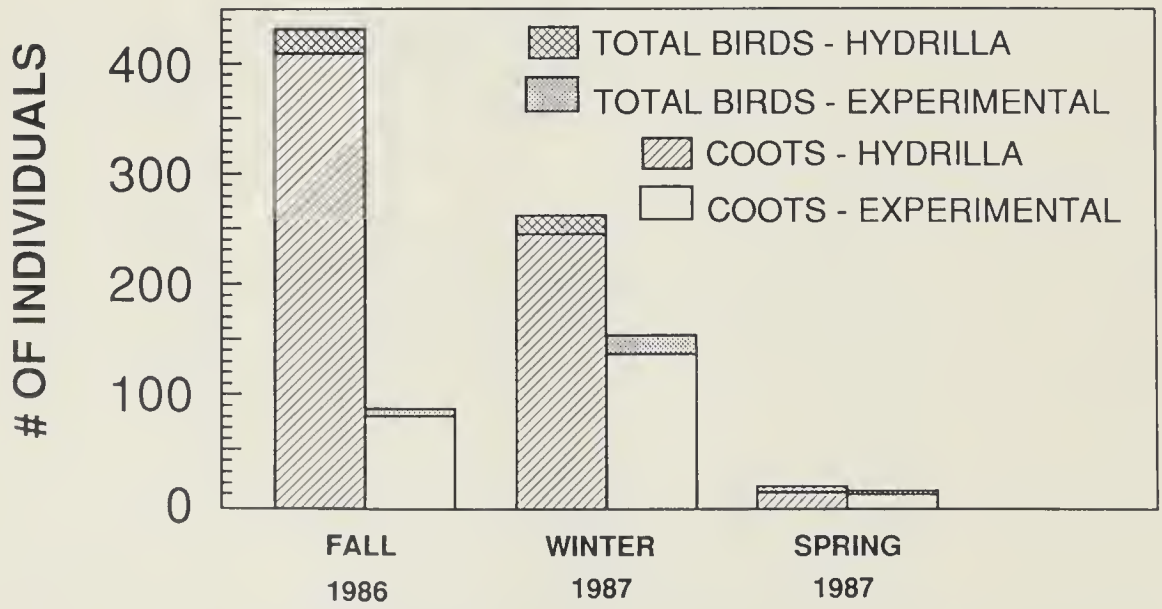

FIG. 2. Total bird numbers and American Coot proportions in hydrilla and experimental plots, Lake Fairfield, Texas, 1986–1987.

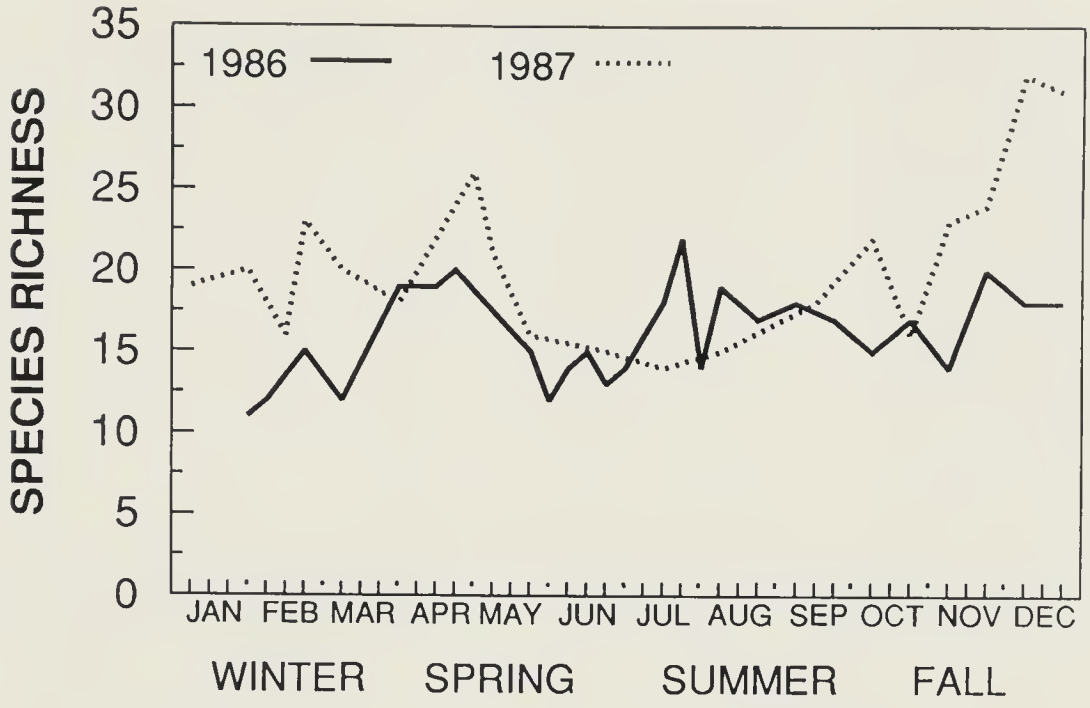

FIG. 3. Bird species richness on Lake Fairfield, Texas, 1986–1987.

and years and was generally higher in 1987 (Fig. 3). Species richness was highest in fall 1987, when the mean number of species per survey was 24.7. This was significantly greater than species richness for all other seasons. Winter 1987 had greater species richness than the corresponding season in 1986. No differences in species richness were detected between years for spring or summer seasons. Much of the increase in species richness in winter and fall 1987 was attributable to increases in duck species richness. In fall 1986, seven species of ducks were observed on the study site, compared to 16 in fall 1987. In winter 1986 and 1987, three and 10 waterfowl species were observed, respectively.

Total bird numbers per survey (Fig. 4) differed across seasons ($F = 9.94$, $P < 0.001$) and was greatest for fall 1987. Fall 1986 and winter 1987 ranked second and third, respectively, and were not different from one another. Winter 1987 did not have more individuals than winter 1986. Spring and summer seasons of both years had fewest individuals and did not differ. Much of the increase in numbers between 1986 and 1987 was attributable to American Coots and ducks.

Results of species and family comparisons across seasons illustrated that most taxa did not vary in abundance between years but exhibited typical seasonal fluctuation due to migration chronology and seasonal changes in habitat use. Several species, however, did show changes in abundance between years. Pied-billed Grebe abundance was higher ($P <$

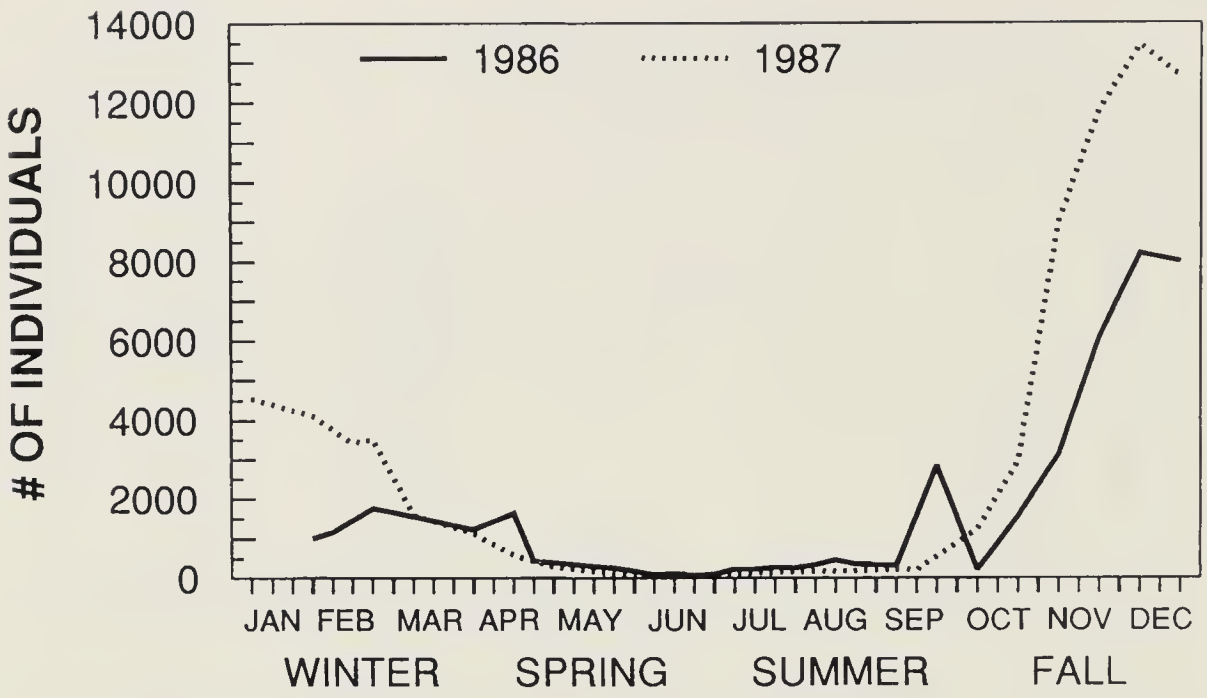

FIG. 4. Total number of individual birds on Lake Fairfield, Texas, 1986–1987.

0.05) in 1987 for winter and fall. American White Pelican (*Pelecanus erythrorhynchos*) abundance in winter was greater ($P < 0.05$) in 1987 than 1986. White Pelicans often were found in hydrilla, although not nearly as much as in open water, making conclusive statements tenuous regarding the effects of increasing hydrilla on the abundance of this species.

Overall duck abundance differed across years. Mean duck abundance in fall 1987 was more than five times that of fall 1986. Species exhibiting significant ($P < 0.05$) increases included Buffleheads (*Bucephala albeola*), Canvasbacks (*Aythya valisineria*), Green-winged Teal (*Anas crecca*), Gadwalls (*A. strepera*), and Ring-necked Ducks (*Aythya collaris*). Mallards (*Anas platyrhynchos*) increased from an average of 6.5 birds per survey in fall 1986 to 164 in fall 1987. Winter 1987 had greater waterfowl abundance than winter 1986. Seven duck species showed increased abundance from winter 1986 to winter 1987. This difference was significant ($P < 0.05$) for Green-winged Teal and Ring-necked Ducks.

Mean American Coot abundance increased by more than four times between winter 1986 and 1987 and two times between falls. Also, coot density in hydrilla increased from 94.8 to 135.4 coots per ha from fall 1986 to fall 1987.

DISCUSSION

Increased hydrilla was the only major habitat change on Lake Fairfield from 1986 to 1987 and may have been the primary factor influencing changes in bird community structure across years. Increases in bird numbers on Lake Fairfield were not a result of local or regional increases. Duck, American Coot, and Pied-billed Grebe numbers, which increased on Lake Fairfield from 1986 to 1987, did not increase on a sample of 108 ponds located within 10 km of the lake (L. A. Reynolds, unpubl. data). Moreover, Christmas Bird Count data (Drennan 1987, 1988) from east-central Texas demonstrate that population increases on Lake Fairfield were not a reflection of region-wide trends.

Birds that showed population increases across years, differential responses to experimental plot treatments, and positive correlations to hydrilla coverage within plots were largely species that have been shown to use hydrilla, including American Coots, Pied-billed Grebes (Esler 1988), and ducks (Johnson and Montalbano 1984, Esler 1988). The increases in species richness demonstrated across years was due largely to ducks.

Many bird populations were unaffected by increased hydrilla coverage. Birds which primarily used any of the other major habitat types did not exhibit population changes. The coverage and quality of other habitats were largely unaffected by hydrilla because hydrilla mainly invaded open water areas. If hydrilla coverage were to increase to the point of dominating most of the open water habitat, birds selecting open water such as Eared Grebes (*Podiceps nigricollis*), cormorants, gulls, terns, and some duck species could be inhibited.

The influence of hydrilla on the bird community was seasonal, due both to the annual chronologies of bird use of the lake and hydrilla growth. Its impact was most important in fall and winter when overall bird abundance was greatest and birds closely associated with hydrilla were present. In spring, both bird and hydrilla abundance were low. In summer, wading birds and birds that utilized open water, such as swallows, gulls, and terns, were prevalent; habitat use data indicated that hydrilla was largely unused by these birds (Esler 1988).

The vegetative structure of Lake Fairfield exhibited horizontal heterogeneity based on concentric rings of habitat types reflecting water depth, which is typical of many wetland basins (Weller and Spatcher 1965). Horizontal heterogeneity has been shown to affect bird community structure in terrestrial systems (Wiens 1974, Roth 1976, Rotenberry and Wiens 1980, Rice et al. 1984, and others), and patchiness and vegetative diversity likewise affect wetland bird communities (Weller 1979, Weller and Voigts

1983). Rice et al. (1984) suggest that the effect of increasing horizontal heterogeneity on bird communities is related to birds' reacting to the addition of patches of suitable habitat rather than to the increase in diversity, per se. The birds of Lake Fairfield likely were reacting to both the increase of vegetative structure in a water body dominated by open water and to the addition of hydrilla specifically. The addition of the layer of hydrilla led to increased foraging opportunities for birds utilizing fish and macroinvertebrates associated with submergents, i.e., Pied-billed Grebes and Northern Shovelers (*Anas clypeata*). However, herbivorous birds may have been reacting to hydrilla, specifically, because of its food value (Montalbano et al. 1978, 1979; Hardin et al. 1984).

Wetlands are dynamic systems, typically experiencing annual fluctuation. Many marsh birds are well adapted to habitat change and quickly respond to variation in resource availability (Weller and Spatcher 1965). Habitat change, in the form of increased hydrilla from 1986 to 1987, resulted in an immediate response by wetland birds in the form of increased species richness and number of individuals. Little evidence for neophobia regarding an exotic species was exhibited, as has been suggested for forest birds (Greenberg 1983).

This study addressed the community changes associated with the invasion of exotics rather than competition between native species and exotics. Posey (1988) stressed that the effect of exotics on natural systems may be indirect and related to habitat change rather than direct competition between natives and exotics. This appeared to be the case on Lake Fairfield, where hydrilla was invading only little-used open water areas, and benefited the bird community through increased vegetative diversity and foraging opportunity. The benefits of hydrilla for wetland birds should be examined when hydrilla management questions arise with both natural and artificial water bodies (Johnson and Montalbano 1987).

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DYNAMICS OF A LOGGERHEAD SHRIKE POPULATION IN MINNESOTA

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Abstract.—We studied breeding pairs of Loggerhead Shrikes (*Lanius ludovicianus*) in Minnesota from 1986–1988 to identify possible causes of declines in midwestern shrike populations. Data on their reproduction and survival were used to construct a stochastic model of the dynamics of a hypothetical Loggerhead Shrike population based on productivity per pair, annual adult survival rate, and annual juvenile survival rate. The model predicted a 20% mean annual rate of decline for the population, which closely resembles an observed 29% decline in breeding pairs in Minnesota from 1986 to 1987. We conclude that declines in migratory midwestern shrike populations are probably caused by factors outside their breeding range. *Received 27 Feb. 1989, accepted 1 Nov. 1989.*

Loggerhead Shrike (*Lanius ludovicianus*) populations are declining throughout the species' range in midwestern, New England and mid-Atlantic states (e.g., Bystrak and Robbins 1977, Hess 1980, Kridelbaugh 1981, Morrison 1981, Burnside and Shepherd 1985). As a result, the Loggerhead Shrike has been included on the National Audubon Society's "Bluelist," and it currently is considered endangered or threatened by many state natural resource agencies. The Loggerhead Shrike is one of the few species showing significant declines in all continental regions of the Breeding Bird Surveys (Robbins et al. 1986).

Inadequate reproduction has been proposed as responsible for this decline (Gawlik 1988, Kridelbaugh 1983, Luukkonen 1987, Porter et al. 1975, Strong 1972). These studies, however, all concluded that reproductive success was normal, and hence not contributing to population declines. Other studies have focused on the possibility of pesticide poisoning (Anderson and Duzan 1978, Busbee 1977, Morrison 1979). Anderson and Duzan (1978) and Busbee (1977) showed that organochlorines can reduce the thickness of shrike eggshells and retard behavioral development of young. Anderson and Duzan (1978) concluded, however, that a slight 2.57% decrease in the eggshell thickness index from 1895 to 1972 was not hindering reproduction. Furthermore, widescale use of organochlorines was curtailed in the early 1970s, yet Loggerhead Shrike numbers have continued to decline.

Loss of habitat on the breeding range has also been addressed as a possible cause for declines in some local populations (Brooks and Temple

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1990, Gawlik 1988, Luukkonen 1987, Kridelbaugh 1983). However, most studies conclude that availability of breeding habitat is not limiting Loggerhead Shrikes.

In this paper we examine the dynamics of a Loggerhead Shrike population in the upper midwest. We use demographic parameters obtained from our field studies and others in a stochastic simulation model that projects trends in population size. This model allows us to identify the rate of decline of a hypothetical shrike population over a 50-year span of time. We compare the results of our simulations with trends detected by the Breeding Bird Survey and other estimators of population trends, and we discuss some possible causes for the continued decline of midwestern shrike populations.

STUDY AREA AND METHODS

The breeding range of the Loggerhead Shrike in Minnesota is restricted primarily to the southern two-thirds of the state (Brooks and Temple 1986). Our field work took place in 11 counties in southern Minnesota during the nesting seasons of 1986, 1987, and 1988. These counties include Benton, Blue Earth, Clay, Dakota, Fillmore, Goodhue, Lac Qui Parle, Morrison, Redwood, Rice, and Sherburne. The dominant vegetative cover types in these 11 counties are agricultural fields and pastures, with small scattered prairie fragments.

From 27 April through 20 August, 1986, we searched for breeding Loggerhead Shrikes in legal townships (i.e., 36 square mile areas) where they had been reported over the previous 10 years. We also investigated reports of shrikes from cooperating observers who had been solicited through the Minnesota Ornithologists' Union and the Minnesota Dept. of Natural Resources. We searched for birds by driving slowly along county and township roads, stopping to scan areas of particularly good habitat (i.e., Brooks and Temple 1986). From 21 April through 15 June, 1987, and from 14 April through 16 May, 1988, we searched for Loggerhead Shrikes in previously occupied breeding territories and adjacent areas. We found nests by observing the behavior of adults or by thoroughly searching all possible nest trees in the area.

In 1986, we established 20-mile- (32-km-) long road transects in each of five counties that had relatively high densities of shrikes (Clay, Sherburne, Morrison, Lac Qui Parle, and Goodhue). Once a week from 4 July through 4 August in 1986 and 1987, we searched for shrikes along these census routes. Observers stopped every ½ mile (804 m) and scanned a ¼-mile- (402-m-) radius circle with binoculars for five minutes.

In 1986 and 1987, we monitored 61 nest sites at 3–5-day intervals until the young left the nest or the nest failed. Each nestling was distinctly marked with colored dye on the breast feathers 1–2 days prior to fledging. Data were collected on clutch size, hatching success (percent of eggs that hatch), fledging success (percent of young that fledge), and nest fate (number of nests that fledged ≥ 1 young). We calculated daily nest survival rates using the "Mayfield method" (Mayfield 1961). Nest success was calculated by raising the daily nest survival rate to the 35th power (i.e., the average length of a nesting cycle). In cases where an entire near-fledging-age brood disappeared simultaneously and fledglings were not observed near the nest site on subsequent visits, we concluded that the nest had failed. Each nestling was banded with a U.S. Fish and Wildlife Service aluminum legband.

Each year we trapped adult shrikes during the breeding season using modified versions of a Bal-Chatri trap (Burger and Mueller 1959) or a Potter trap (Blake 1951). Lab mice and

Zebra Finches (*Taeniopygia guttata*) were used as lures in the traps. In 1986, 1987, and 1988, we trapped 9%, 29%, and 32% of the known adults, respectively. We concentrated trapping efforts in areas where we had banded birds in previous years. Trapping efforts were greater in 1987 and 1988 than in 1986. In 1988, 80% of our trap attempts were made in territories where birds were banded in 1987.

We constructed a stochastic model of the dynamics of a hypothetical Loggerhead Shrike population based on productivity per pair, annual adult survival rate, and annual juvenile survival rate. Productivity was a normally distributed stochastic function with a mean value taken from our data. We assumed that all adult birds breed, as we found no evidence of nonbreeders in our population, even though we had a good likelihood of finding them if they existed. Annual adult survival was a normally distributed stochastic function. We used territory reoccupancy rates from our study to estimate the annual adult survival rate, the assumptions being that males return to their previous breeding territory if they survive the winter, that male survival rate equals female survival rate, and that there is always an even sex ratio. There are no estimates of annual survival rates for juvenile Loggerhead Shrikes. Therefore, in our model, first-year survival rate was assumed to be a fraction of the adult survival rate for that year. We used the mean ratio of juvenile-to-adult survival calculated from Woolfenden and Fitzpatrick's (1984) data on Scrub Jays (*Aphelocoma coerulescens*), a similar-sized passerine, to estimate the mean value of this fraction. We multiplied that fraction, which is a normally distributed stochastic function, by our estimate of adult survival to estimate juvenile survival rate each year. Because there are no long-term studies (>5 years in duration) of year-to-year variations in shrike population parameters, we used results of Woolfenden and Fitzpatrick's (1984) long-term study of Scrub Jays to estimate the coefficients of variation of our model parameters.

Our model begins with a population of breeding shrikes and then predicts the population's size in subsequent years using the following equation:

$$N_t = N_{t-1}(S_a) + N_{t-1}(P/2)(S_j)$$

where N_t = size of the breeding population in year t, S_a = annual survival rate of adults, S_j = annual survival rate of juveniles, and P = number of young raised per breeding pair. During each annual cycle, a value for productivity and annual survival rate of adult birds is stochastically determined by randomly selecting a value from a normally distributed pool of values with a mean based on our field data and a coefficient of variation derived from the literature. A value for juvenile survival rate is stochastically determined by randomly selecting a value for the ratio of juvenile-to-adult survival, whose mean and coefficient of variation are taken from data on Scrub Jays, and multiplying it by the adult survival rate for that year. We ran our model 100 times and each time observed the change in population size over 50 years.

RESULTS

We collected nesting data on 48 breeding pairs of Loggerhead Shrikes in Minnesota during 1986 and 1987. The pairs were scattered throughout 11 counties and occurred at low densities. In 1986, 29 pairs of shrikes made 34 nest attempts, and in 1987, 19 pairs made 27 nest attempts. Most of the second nest attempts resulted after a failed first nest attempt. Five (10%) of the 48 pairs attempted to raise second broods; four of them were successful. In 1986, 24 breeding pairs were found along five 20-mile (32-km) survey routes. In 1987, 17 breeding pairs were found along these

TABLE 1
LOGGERHEAD SHRIKE NESTING DATA FROM MINNESOTA, 1986–1987

Parameter	Mean ± SD or percentage (N)		
	1986	1987	Both years
Clutch size	5.58 ± 1.38 (24)	5.73 ± 0.94 (22)	5.65 ± 1.17 (46)
Nestlings per nest	4.54 ± 2.20 (26)	3.80 ± 2.45 (25)	4.18 ± 2.33 (51)
Fledglings per nest	3.12 ± 2.17 (33)	2.89 ± 2.10 (27)	3.02 ± 2.17 (60)
Fledglings per pair	3.48 ± 1.91 (29)	4.11 ± 1.74 (19)	3.73 ± 1.82 (48)
% Hatching success	81 (24)	71 (22)	76 (46)
% Fledging success	66 (26)	77 (25)	72 (51)
% Nests that fledged >1 young	74 (34)	70 (27)	73 (61)
% Pairs that fledged >1 young	83 (29)	84 (19)	83 (48)
Mayfield estimate of nest success (%)	66 (24)	56 (23)	62 (47)

same survey routes; the surveyed population had experienced a 29% decline in one year.

Productivity data.—The mean clutch size was 5.65 ± 1.17 [SD], (N = 46), ranging from a minimum of three eggs to a maximum of seven eggs. The modal clutch size was six. On average, 4.18 ± 2.33 eggs hatched per nest (N = 51), 3.02 ± 2.07 young fledged per nesting attempt (N = 60), and 3.73 ± 1.82 young fledged per pair (N = 48). There were no significant differences between years in clutch size, number of eggs hatched, number of young fledged per nest, or number of young fledged per pair ($P > 0.10$ in all cases, students t-test). See Table 1 for a summary of nesting parameters.

Of 48 pairs of shrikes, 40 (83%) successfully fledged at least one young. However, because of renesting attempts, only 74% of all nest attempts successfully fledged at least one young. Hatching success was higher in 1986 (81%) than in 1987 (71%) ($\chi^2 = 3.006$, $0.10 > P > 0.05$). However, fledging success was lower in 1986 (66%) than in 1987 (77%) ($\chi^2 = 2.940$, $0.10 > P > 0.05$). On average, 55% of eggs laid resulted in fledged young. Using Mayfield's estimate of reproductive success based on exposure days, we calculated a reproductive success of 62% (Table 1).

Survival data.—We found 37 occupied territories in 1986, 22 in 1987, and 16 in 1988. In 1987, 15 (41%) of the 37 breeding territories used the previous year were reoccupied; in 1988, 13 (59%) of the 22 breeding territories used in 1987 were reoccupied. When both seasons' data were combined, the average reoccupancy rate was 47%.

TABLE 2
PARAMETERS IN A MODEL OF THE DYNAMICS OF A HYPOTHETICAL LOGGERHEAD SHRIKE POPULATION

Model parameter	Mean value	Coefficient of variation (%)[a]
Productivity per pair	3.73	29
Annual adult survival	0.47	11
Ratio of juvenile to adult survival	0.41[a]	22
Annual juvenile survival	0.19	36

[a] From Woolfenden and Fitzpatrick (1984).

We trapped and banded 25 adult Loggerhead Shrikes. Of the five territories in which we had banded adults in 1986, one was reoccupied in 1987. In 1988, eight of 10 territories occupied by banded adult birds in 1987 were reoccupied; we successfully trapped at least one adult at each of seven of these territories. Seven of the banded adults from 1987 were males, and three (43%) of these banded males returned to reoccupy their previous year's territories. We neither trapped nor observed in subsequent years any of the 196 shrikes we banded as nestlings in 1986 and 1987.

Population modeling.—Table 2 summarizes the model parameters and their corresponding coefficients of variation. Based on 100 simulations, the model predicted a 20% (range 14–30%) mean annual rate of decline for the hypothetical Loggerhead Shrike population. This rate of decline leads to a halving of the population's size every 3.5 years.

To determine which of the demographic parameters had the greatest influence on the rate of change in population size, we tested the sensitivity of the model to changes in each of its components. We sequentially multiplied each model parameter's mean by 105%, while holding the other two variables constant, and ran the model 100 times. The population's rate of change decreased by 15% (i.e., from 20% to 17%) in response to a 5% increase in each of the model's parameters. Thus, each of the parameters exerted the same amount of influence on the rate of change in population size.

DISCUSSION

Shrike demography.—Reported values of nesting success of shrikes range from 43% in Alabama (Siegel 1980) to 80% in Illinois (Graber et al. 1973). The lowest value, 43%, is well below the second lowest value of 62% (Luukkonen 1987), indicating that values greater than 60% are more typical of Loggerhead Shrike nesting success. Ricklefs (1973) notes

that nest success of temperate zone passerines with open nests averages 47%, suggesting that Loggerhead Shrikes have relatively high reproductive success for a passerine.

The number of young produced per female in Minnesota (3.73) closely resembles values from other recent shrike studies (Erdman 1970, Porter et al. 1975, Gawlik 1988). Data from our study and others suggest that Loggerhead Shrikes are experiencing typical nesting success for an open-nesting passerine species in the temperate zone.

Because there have been no long-term studies of marked shrike populations, our estimates of survival rates must be inferred. Using territory reoccupancy rate to estimate annual adult survival assumes that those males that did not return to their previous year's territories are dead. Although we cannot strictly test this assumption, our reoccupancy rate (47%) did closely resemble our adult male band-return rate (43%), indicating that the assumption is valid. Kridelbaugh (1983) reported that 47% of banded male shrikes returned to their territories of the previous year and that 54% of the previous year's territories were reoccupied. Likewise, A. Blumton (pers. comm.) reported a 50% return rate of banded adult shrikes in Virginia. Ricklefs (1973) notes that adult survivorship is generally low among small land birds (40–60% in most temperate passerines). Our estimate of adult survival is, therefore, not at all unusual for a temperate zone passerine.

There are few data that reveal the relationship between adult and juvenile survival rates in passerines. We calculated juvenile survival to be, on average, 41% of the adult survival rate, based on data from Woolfenden and Fitzpatrick's (1984) study of Scrub Jays. Ricklefs (1973) states that, in general, juvenile survival rates of passerines are typically one-quarter to one-half of the adult survival rate. Our estimate of juvenile-to-adult survival ratio is typical of values for other passerines.

The annual survival rates of adult and juvenile Loggerhead Shrikes in the upper midwest, despite being within the range typical of passerines, are too low to maintain population stability. Henney et al. (1970, Table 1) provides a deterministic model which estimates the productivity per pair required to maintain a stable population, given survival rates for adult and juvenile age classes. If our population is surviving at average rates of 47% and 19% for adults and juveniles, respectively, approximately 5.5 young must be produced per pair. No shrike population is known to produce this many young, which would require almost 100% nest success or consistently successful double brooding.

Because our Minnesota shrike population is achieving good fledging success, and habitat conditions on the breeding range seem more than adequate to accommodate the present population (Brooks and Temple

1986), it seems likely that survival of birds while they are on the summer breeding range is also good. We found no evidence of adult mortality during the breeding season, and survival of post-fledging birds for two weeks post fledging seemed to be high, although we did not precisely estimate it. Overwinter survival on the nonbreeding range is, therefore, a likely point in the shrike's annual cycle to look for evidence of problems. In a six-year study of a declining population of Red-backed Shrikes (*Lanius collurio*) in Britain, Ash (1970) suggested that reductions in annual survival rates were responsible for that population's decline, rather than a reduction in the production of young.

Possible causes of low overwinter survival.—Although the exact location of our Minnesota population's wintering quarters is yet unknown, Burnside (1987) found that banded shrikes from northern mid-continental populations have been recovered during the winter in Texas, Arkansas, Oklahoma, Mississippi, Louisiana, Kansas, and Missouri. Root (1988) showed, in an analysis of Christmas Bird Count data, that the highest concentrations of wintering Loggerhead Shrikes are found in the gulf coast states, primarily Texas, Louisiana, Mississippi, and Alabama.

Burnside and Shepherd (1985) suggested that recent land-use changes have eliminated prime shrike habitat in Arkansas. Kridelbaugh (1981) attributed the decline of the Loggerhead Shrike in Missouri to the conversion of pastureland and hayfields to row crops. The extensive conversion of pastureland and old fields to cereal-crop production has resulted in the elimination of large areas of grassland habitat throughout the gulf coast and adjacent regions (Neff and Meanley 1957; USDA 1950, 1975, 1986).

There is good evidence indicating that these habitat changes have impacted populations of birds that winter in the region. The best documented population responses have been dramatic increases in species that feed on grain, notably members of the family Icteridae (Stepney 1975). Because these wintering blackbirds feed primarily on cultivated grains, their populations have steadily increased over the same 50-year period that shrike populations sharing the same wintering areas have steadily decreased (Temple and Temple 1976, Brittingham and Temple 1983).

The impact of this loss of wintering habitat for migrating shrikes from northern breeding areas is made even more threatening by the presence of resident shrike populations throughout these southern states (Miller 1931). Southern populations of shrikes are nonmigratory and defend winter territories (Gawlik 1988, A. Blumton, pers. comm.). Habitat alterations in the gulf coast region and adjacent states have apparently reduced the habitat available for resident shrikes; their populations have declined (Robbins et al. 1986, Burnside 1987), although not as severely as more

northerly populations. If resident shrike populations are being limited by habitat availability, migrant shrikes wintering in the same area are almost certainly being forced to occupy marginal habitats that are not being held by territorial residents, and this reduces overwinter survival to inadequately low levels.

Population declines.—The possibility that a local or regional shrike population could decline and become extirpated within a few decades is an alarming prospect, but Anderson and Duzan (1978) provide evidence of one such extirpation of a local population of Loggerhead Shrikes in central Illinois. The results of the Breeding Bird Survey indicate that the entire upper midwestern shrike population (including the states of Minnesota, Iowa, Illinois, Wisconsin, Michigan, and Indiana) has been declining at a rate of 6% per year from 1966–1987 (Robbins et al. 1986, S. Droege, pers. comm.). Our data suggest even more severe declines in local populations in Minnesota.

Our population model, although requiring the use of several key assumptions about shrike demography, strongly suggests that the causes of declines in midwestern shrike populations are probably associated with overwinter survival. Research attention should now focus on learning more about midwestern shrikes on their wintering areas and how habitat management there could reduce the population's rate of decline. It seems unlikely that conservation efforts on midwestern breeding areas will succeed in slowing or reversing the declines in these shrike populations if they are being limited by factors on their nonbreeding range.

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THE BIRDS OF RUM CAY, BAHAMA ISLANDS

DONALD W. BUDEN[1]

ABSTRACT.—Seventy species of birds are recorded from Rum Cay, 31 for the first time. Of the 38 probable breeding species, 17 are land birds. Most of the breeding species are widespread in the Bahamas generally, and no species or subspecies is endemic to Rum Cay. Nests, eggs, and young are reported for 21 species, all first breeding records for the island. The Pearly-eyed Thrasher (*Margarops fuscatus*) was the most common bird during the summer 1989 census. *Received 11 Sept. 1989, accepted 1 Dec. 1989.*

The avifauna of Rum Cay has never been reviewed systematically, and the ornithological literature consists mainly of a few brief notes from the late 1800s and early 1900s. The present paper is based largely on my observations during 25 May–9 July 1989, and it includes information summarized from the literature, data from museum labels and catalogs, and previously unpublished notes contributed by other observers.

STUDY AREA

Rum Cay is a small (16 km long, 78 km^2), low (maximum elevation ca 37 m) limestone island in the east-central Bahamas (Figs. 1 and 2). Shoal water extends only a short distance offshore, and the island, in effect, sits on its own bank never having been connected over land to adjacent islands during even the lowest Pleistocene sea level minima. The coast consists of alternating stretches of both sandy and rocky beaches and cliffs to ca 25 m high, highest along the eastern and southeastern shores.

Coastal vegetation includes strand and sparse scrub mainly on sand, and low, dense scrub mainly on rock. Coconut palms (*Cocos nucifera*) are common in Port Nelson but scarce elsewhere, and casuarinas (*Casuarina equisetifolia*) are most numerous along the southern shore. The interior is covered mainly by dense scrub consisting of bushes and small trees about 3–5 m tall. Patches or pockets of xeric-to-semimesic woodland with trees to ca 20 m tall occur mainly on the slopes of ridges and at both permanent and temporary freshwater ponds. Among the more common large trees of the interior are mahogany (*Swietenia mahagoni*), poison wood (*Metopium toxiferum*), wild tamarind (*Lysiloma latisiliquum*), wild oak (*Bucida buceras*), and an unidentified species of *Coccoloba,* probably pigeon plum (*C. diversifolia*).

Numerous salt ponds typically are bordered by buttonwood (*Conocarpus erectus*), black mangrove (*Avicennia germinans*), and, to a lesser extent, red mangrove (*Rhizophora mangle*). The latter is more common along the shores of Lake George, a large, clear salt lake with subterranean connection(s) to the sea, and the Port Nelson salt lake, which has a narrow tidal channel on its eastern shore.

Permanent freshwater ponds are much less common. At least two of the three I visited consisted of freshwater lenses on saline bases subject to tidal flow. These ponds typically

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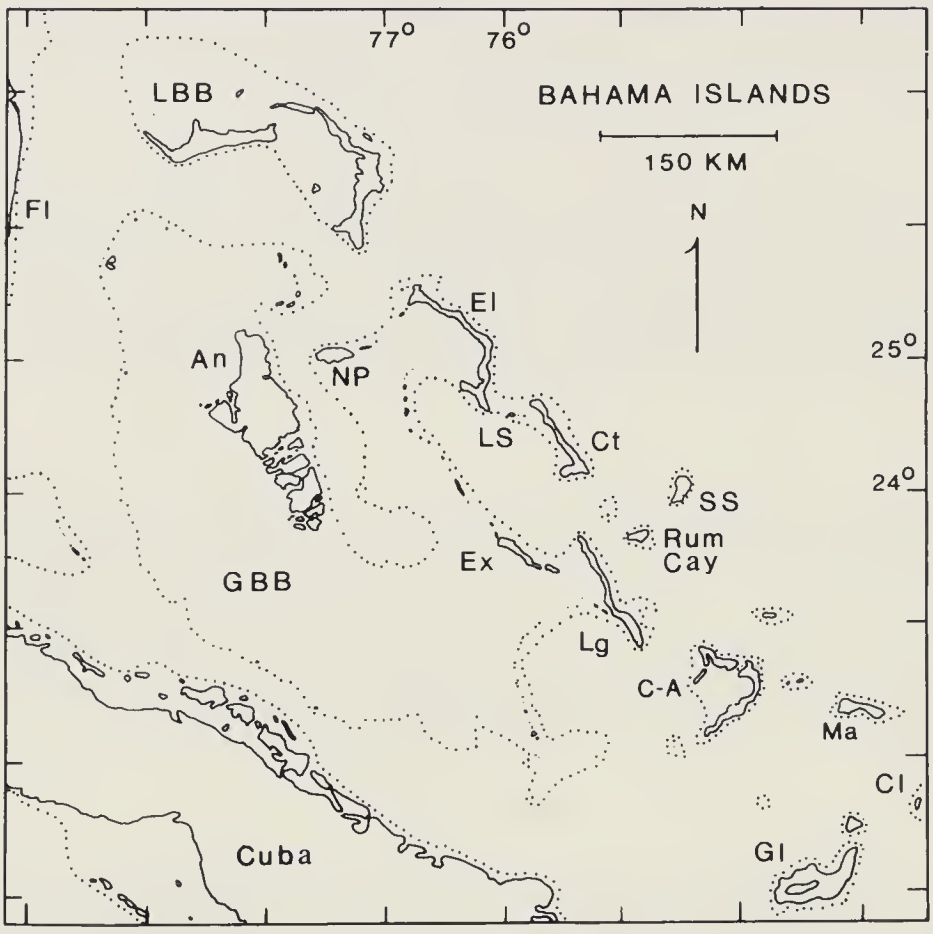

FIG. 1. Map showing the location of Rum Cay and other Bahama Islands; dotted lines denote the 100 fathom contour. An = Andros, CI = Caicos Islands, El = Eleuthera, Ex = the Exumas, Fl = Florida, GBB = Great Bahama Bank, GI = Great Inagua, LBB = Little Bahama Bank, Lg = Long Island, LS = Little San Salvador, NP = New Providence, SS = San Salvador.

are bordered by large trees and have dense growths of cattail (*Typha*) and leather fern (*Acrostichum*). Sabal palm (*Sabal palmetto*) and pond apple (*Anona glabra*) also are common here and in low-lying, swampy areas, which were dry during my visit. Some of the low areas that collect rainfall in temporary ponds have almost pure stands of *Bucida buceras,* the largest trees being ca 20 m tall and nearly 2 m in diameter at ground level. The large, trunk-like limbs (to ca 0.5 m in diameter) diverge from the main trunk one to two meters above the ground, and the sprawling branches are festooned with bromeliads. These woods are park-like in appearance as the broad-crowned trees are widely spaced (ca 15–20 m) and the ground cover and other vegetation are low and generally sparse. Broad areas of sedge (*Eleocharis*) occur in these seasonally flooded basins.

I estimated approximately 100 people resident on Rum Cay during my visit, all in Port Nelson; Bowman (1976) reported 93 censused in 1975. During the 1800s and into the early 1900s, the population ranged from several hundred to nearly 1000 (858 in 1851) and was distributed over five principal settlements, all but Port Nelson now in ruins (Bowman 1976). Bowman considered the decreased demand for sisal fiber (supplanted by synthetics) and devastations to the salt and pineapple industries by hurricanes (those of the mid-1920s were especially damaging) among the chief factors contributing to the island's decline. Areas

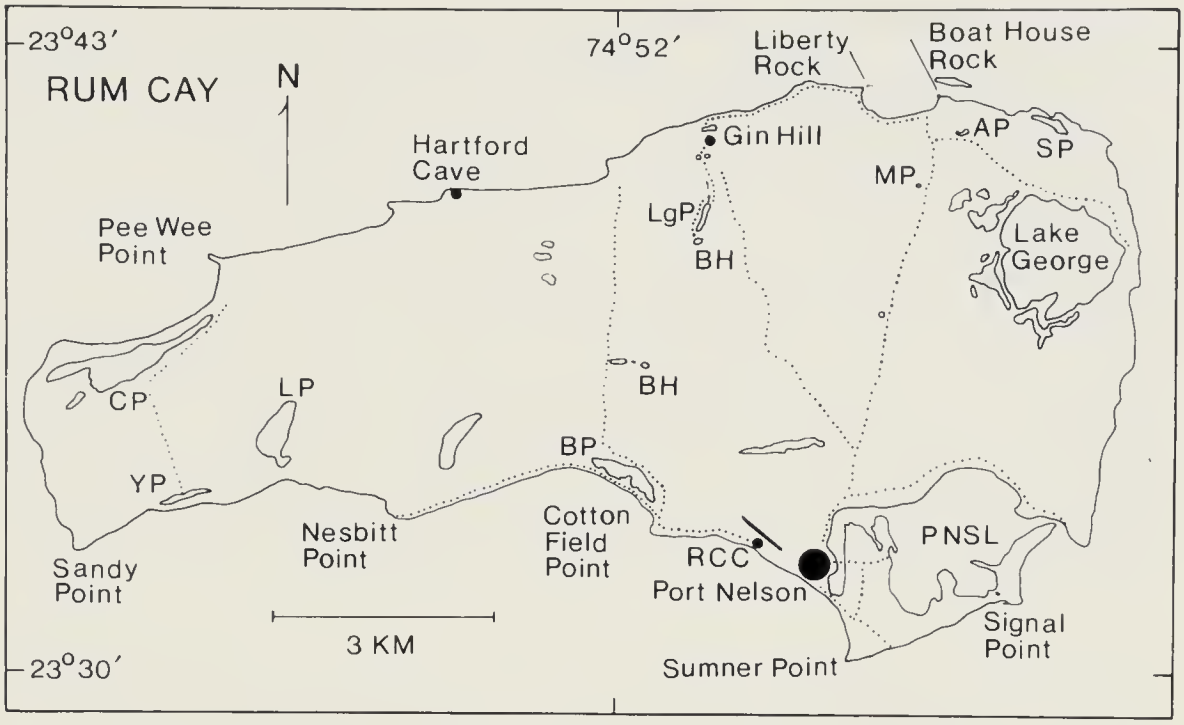

FIG. 2. Map of Rum Cay. Dotted lines show routes followed on census walks. Heavy solid line indicates airstrip. AP = Adderley's Pond, BH = Blue Hole, BP = Bay Pond, CP = Carmichael Pond, LP = Line Pond, LgP = Long Pond (local name not in map references cited), MP = Mermaid Pond, PNSL = Port Nelson Salt Lake, RCC = Rum Cay Club, SP = Shad Pond, YP = Yard Pond.

under cultivation in past decades have since reverted to scrub, and agriculture presently is limited to a few, small gardens in and around Port Nelson. Feral populations of cattle (once raised for both meat and milk), goats, and cats roam the island, being most numerous on the eastern half.

Narrow, unpaved roads circumscribe and traverse the island. The one from Port Nelson to the north side has been widened and is well-maintained. The others, for the most part, have not been maintained for decades. They are overgrown, and many are difficult to use even as foot paths. Bahama haulback (*Mimosa bahamensis*), a bushy plant with extremely sharp, recurved spines, is common throughout the island, especially in cut-over areas, and it makes travel off maintained trails extremely difficult.

Climatological data for Rum Cay generally are lacking. However, beginning in January 1988, D. Melville has kept monthly records of rainfall using a Taylor 11″ Clear-Vu Rain Gage. He recorded 44.97 inches for 1988, of which 21.39 inches fell during January–June, 7.38 inches just in June. Only 4.82 inches have been recorded January–June 1989, with no measurable precipitation during June. Many of the ponds were dry during my visit and much of the scrub was parched and withered.

ORNITHOLOGICAL HISTORY

Ridgway's (1891) list of 27 species of birds collected on Rum Cay by the naturalists of the *Albatross* Expedition in March 1886 is the first report on the avifauna of the island. Ridgway did not state what days the expedition was on Rum Cay, but the collecting dates for 26 of 27 species fall within the period 1–6 March (11 Bahama Mockingbirds [*Mimus*

gundlachii] were reported taken during 1–29 March); all specimens were deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Riley (1905a) reported on the 15 species observed by the Geographical Society of Baltimore Expedition on 10 July 1903, and W. W. Worthington (in Todd and Worthington 1911) commented briefly on Killdeer (*Charadrius vociferus*) (p. 449) and Pearly-eyed Thrasher (*Margarops fuscatus*) (p. 475) seen on 28 January 1909, during a Carnegie Museum Bahama Expedition.

J. C. Greenway, Jr. stopped at Rum Cay on 15 February 1934, enroute to the Antilles aboard the *Utowana*. He collected one specimen each of the Zenaida Dove (*Zenaida aurita*) and the Pearly-eyed Thrasher for the Museum of Comparative Zoology, Harvard University (MCZ). Albert Schwartz and Richard Thomas visited Rum Cay mainly to collect reptiles, but they also obtained 11 study skins of seven species of birds during 17–20 June 1966—specimens now in the Louisiana State University Museum of Natural Science. Mary H. Clench was on the island 7–9 March 1976 on a Carnegie Museum Bahama Expedition. Her field notes cover 26 species and include many new locality records mentioned in the present report. Alexander Sprunt IV visited Rum Cay briefly during 13–14 May 1985, contributing two new locality records of migrant shorebird species to this study.

METHODS

English names and binomials follow the nomenclature of the American Ornithologists' Union (1983, 1989), but placement of the Greater Flamingo follows Olson and Feduccia (1980). Subspecies names are used only in selected cases and follow Bond (1956) unless indicated otherwise. Abbreviations of names of observers or collectors are AS = Albert Schwartz, DWB = Donald W. Buden, MHC = Mary H. Clench. Questionable records and those of extirpated populations are in brackets.

Abundance is based largely on numbers of individuals usually seen during a day in the field: VC = very common, 30 or more/day; C = common, 15–30/day; FC = fairly common, 5–15/day; UC = uncommon, 1–5 on most days, but not seen every day; S = scarce, 5–15/season; and R = rare, 1–5/season.

Residents occur year-round and breed, and summer visitors breed but are less numerous or absent in winter. Nonbreeding visitors are chiefly winter visitors or transients from continental North America, but include occasional visitors or vagrants as well as species present throughout the year but not breeding. In cases where records are especially scanty and status is uncertain, "probable" or "possible" status is inferred from records for nearby islands relying largely on Bond (1956), Brudenell-Bruce (1975), Buden (1987a, 1987b), and Miller (1978).

Censuses were done by recording all birds seen and heard calling along 12 different routes (mainly roads and trails) covering 42 km during 26 May–8 July 1989. Surveys were at different times of the day from dawn to dusk. Eleven of the routes were surveyed from one to seven times, but the 6.5 km between Port Nelson and the north side were covered 26 times. In cases where routes were surveyed more than once, the maximum number of individuals recorded during one survey was used to calculate abundance. Distances were estimated from a Bahamas Government map (Lands and Surveys Department 1972). Dimensions for Rum Cay are from the Ministry of Education (1985).

All previous locality records are included for nonbreeding visitors, as well as for rare, scarce, and uncommon residents and summer visitors, and for species whose status is uncertain. A species recorded on Rum Cay for the first time is indicated by an asterisk.

SPECIES ACCOUNTS

Least Grebe (*Tachybaptus dominicus*).—Uncommon to fairly common resident, and usually seen at small ponds with densely vegetated shores—

maximum six together at Long Pond, 23 June 1989 (DWB). Two collected on 2 and 3 March 1886 (Ridgway 1891), and "two were seen on a small lake," 10 July 1903 (Riley 1905a). Breeding is unconfirmed, but very probable. I saw one pair courting several times on Mermaid Pond during mid-June, and the birds were present at the pond throughout my stay from late May to early July 1989.

Pied-billed Grebe (*Podilymbus podiceps*).*—Status uncertain, possibly resident. Several were observed during May–July 1989, mainly at salt ponds (DWB).

White-tailed Tropicbird (*Phaethon lepturus*).*—Common to locally very common summer visitor. Usually seen near coastal cliffs in groups of 5–20, most numerous along the northeastern shore. Breeds in crevices and recesses in cliffs and caves, in sheltered areas beneath boulders, and in deeply eroded pockets in beach rock: 13 clutches (six eggs, seven downy young) between Pee Wee Point and the central part of the eastern shore, 26–31 May 1989, and one egg at Liberty Rock, 23 June 1989; 100–150 breeding pairs estimated during May–July 1989 (DWB).

Double-crested Cormorant (*Phalacrocorax auritus*).*--Status uncertain. Present in small numbers on the larger salt ponds—maximum seven together at Bay Pond on 17 June, and eight together in mangroves on the southeastern shore of Lake George, 26 June 1989 (DWB). All the cormorants I observed at close range had the diagnostic characteristics of *P. auritus,* including crooked neck in flight, relatively large, orange-colored gular pouch, and short tail.

Magnificent Frigatebird (*Fregata magnificens*).*—Nonbreeding visitor. Two sight records only: an unstated number seen 10 July 1903 (Riley 1905a), and one seen soaring high over the eastern shore, 29 May 1989 (DWB).

Great Blue Heron (*Ardea herodias*).*—Nonbreeding visitor. One seen by MHC during 7–9 March 1976 is the only record.

Little Blue Heron (*Egretta caerulea*).*—Nonbreeding visitor. The one I saw at Boat House Rock on 27 June 1989 is the only record. Squalls that passed across the northern part of Rum Cay from the west the previous night may have carried it from Long Island, ca 30 km to the west. When flushed from its perch, the bird flew westward slowly against the wind about 1 km, climbing to about 100 m. It then slowly drifted back over Boat House Rock maintaining altitude and gradually disappeared from view far to the east.

Tricolored Heron (*E. tricolor*).*—Fairly common at salt ponds and probably resident, but breeding is undocumented. Usually seen singly or in groups of two to four—maximum 11 together at Bay Pond, 17 June 1989 (DWB).

Reddish Egret (*E. rufescens*).*—Status uncertain. Possibly a scarce res-

ident. I saw probably fewer than ten individuals (all of them white phase) occasionally during May–July 1989—maximum four together in a salt pond west of Lake George, 25 June 1989.

Cattle Egret (*Bubulcus ibis*).*—Status uncertain. Possibly breeding in small numbers. I saw no more than two together occasionally during June, mainly near the airstrip, and D. Melville (pers. comm.) has seen *B. ibis* in the vicinity of the Rum Cay Club from time to time during the past ten years.

Green-backed Heron (*Butorides striatus*).—Common resident in aquatic habitats throughout and often seen in scrubland far from water. The commonest of the herons. Breeding.—One nest with two ambulatory but flightless young on a small red mangrove island ca 3 m off the southwestern shore of Lake George, 5 June 1989 (DWB).

Yellow-crowned Night-Heron (*Nyctanassa violacea*).*—Fairly common resident although breeding is undocumented. Usually seen along beaches and near ponds, occasionally in scrublands.

West Indian Whistling-Duck (*Dendrocygna arborea*).*—Probably resident, but breeding is undocumented. A flock of 10–15 was seen at Yard Pond, 1 June 1989, and 43 were counted at a small (ca 70 m in diameter) freshwater pond (identified as a "blue hole" on a Bahamas Government map—see Lands and Surveys Department 1972) approximately 2.5 km north of Cotton Field Point, 21 June 1989 (DWB). This blue hole also had a large number of White-cheeked Pintails (see account below). I collected the mummified, partial remains of a West Indian Whistling-Duck (USNM 612543) near a small, mangrove-fringed pond at the western end of the airstrip, 10 June 1989. Bobby Little, pilot for the Rum Cay Club, believed it probably was one among the occasional avian casualties caused by collisions with incoming aircraft.

White-cheeked Pintail (*Anas bahamensis*).*—Common to very common resident or summer visitor—maximum ca 75 together at Bay Pond, 25 May 1989, and 123 counted at a small, freshwater "blue hole" approximately 2.5 km north of Cotton Field Point, 21 June 1989 (DWB). The lack of sightings on previous surveys suggests *A. bahamensis* may be absent or much less common on Rum Cay in winter. Breeding.—Three or four flightless young were observed being led to safety by an adult in a swampy area near the northern end of Long Pond, 23 June 1989 (DWB).

[Greater Scaup (*Aythya marila*).—The one record requires confirmation. According to Ridgway (1891), naturalists aboard the *Albatross* collected one *A. marila* on Rum Cay and another on San Salvador on unspecified dates in 1886. Bond and Friedman (Bond 1958) considered these records doubtful as neither specimen could be found in the USNM collections (though one was cataloged under the number 108935), and because Ridg-

way (1891) had not listed the very similar *A. affinis,* a common winter duck in the Bahamas and Greater Antilles (Bond 1971a) among the birds collected on the expedition. To the best of my knowledge, the only unquestionable record of a Greater Scaup from the West Indies was reported by Bond (1971b) who, with F. Gill, examined the wing of one shot on New Providence and obtained from the hunter by a local naturalist, Paul Dean, on 31 January 1971.]

Osprey (*Pandion haliaetus*).*—Rare resident. Two or three examples of the resident "West Indian subspecies," *P. h. ridgwayi,* were seen occasionally during May–July 1989, mainly on the northern and southeastern coasts, and the partial skeleton of an Osprey (USNM 612546) was collected on a rocky beach on the eastern shore, 29 May 1989 (DWB). Breeding.—A nest on a ledge at Signal Point was empty during my visits in June, but one of the residents of Port Nelson said it contained two young earlier in the year. I found another presumably recently active nest on top of a large rock several meters off the eastern shore (near where the skeleton was recovered) and the apparently storm-wrecked remains of another nest at Pee Wee Point. Residents of Port Nelson told of a large nest on the telecommunications tower that was in use for many years until company servicemen removed the nest sometime in the mid-1980s. This nest was present when the Carnegie Museum Expedition visited the island in March 1976, but no Ospreys were seen then (MHC).

American Kestrel (*Falco sparverius*).*—Fairly common resident, most numerous in the vicinity of Port Nelson. Breeding.—Three flightless young (with scattered patches of down and incompletely emerged flight feathers) in a vertical hole (ca 0.5 m deep, 10–15 cm wide at entrance and much wider below) in beach rock near the tide line, ca 0.5 km west of Yard Pond, 15 June 1989 (DWB); also, several territorial birds apparently nesting in the tops of coconut palms in Port Nelson, and other aggressive individuals (swooping in attack) in the vicinity of coastal cliffs, all during May–July 1989 (DWB).

Clapper Rail (*Rallus longirostris*).*—Probably an uncommon resident in mangroves throughout, most numerous at the Port Nelson salt lake. One seen at the salt lake on 3 June and another on 24 June 1989; one seen at Adderley's Pond, 4 July 1989, and several others heard calling at different localities during May–July 1989 (DWB).

Common Moorhen (*Gallinula chloropus*).*—Scarce to uncommon resident, mainly in aquatic habitats with dense, weedy, shoreline vegetation. One seen at Yard Pond, 1 June, four others at a small pond just west of the blue hole north of Cotton Field Point, 21 June, and two others at Long Pond on 23 June 1989 (DWB). Breeding.—One nest containing six eggs and constructed of twigs and sparsely lined with leaves in a basin-

shaped rock at the base of a stone wall crossing Yard Pond, 1 June 1989 (DWB).

American Coot (*Fulica americana*).—Probably a nonbreeding visitor, two were collected 2 and 3 March 1886 (Ridgway 1891) and hundreds were seen at times during winter (D. Melville).

Black-bellied Plover (*Pluvialis squatarola*).*—Nonbreeding visitor. Seen on beaches occasionally during May–July (DWB). Doubtless occurring in winter but no records.

Snowy Plover (*Charadrius alexandrinus*).*—Probably a rare resident or summer visitor. Approximately eight adults (maximum four together) and one young seen at Carmichael Pond on 31 May and 15–16 June 1989 (DWB). Breeding.—One downy young with adult in attendance at the western end of Carmichael Pond, 16 June 1989 (DWB).

Wilson's Plover (*C. wilsonia*).—Fairly common in summer along shores of shallow ponds and on sandy beaches—maximum eight together at a small pond west of Lake George, 25 June 1989 (DWB). Breeding probable but not confirmed, though Riley (1905a) reported that "a pair were evidently nesting on Rum Cay, July 10 [1903]." No winter records, but recorded elsewhere in the Bahamas then (Brudenell-Bruce 1975, Buden 1987b).

Semipalmated Plover (*C. semipalmatus*).*—Nonbreeding visitor. One seen at Bay Pond, 25 May, and another at Adderley's Pond, 29 May 1989 (DWB).

Killdeer (*C. vociferus*).—Fairly common at shallow ponds throughout, and more numerous in summer than in winter. An unstated number seen on 28 January 1909 (Worthington in Todd and Worthington 1911), three seen during 7–9 March 1976 (MHC), and many observed during May–July 1989 (DWB). Breeding.—A pair copulating at Adderley's Pond, 9 June, three downy young with one adult in attendance at Mermaid Pond, 20 June 1989, and a presumed nesting bird feigning a broken wing at a dried-out pond on the north side of Gin Hill, 2 July 1989 (DWB). Summer records probably all pertain to the "West Indian subspecies," *C. vociferus ternominatus,* whereas others may be *C. v. ternominatus* or examples of the nominate race, which occurs throughout the West Indies in winter (Bond 1956). Worthington's January record (in Todd and Worthington 1911) is listed under the nominate race, but sight records of these subspecies are unreliable.

American Oystercatcher (*Haematopus palliatus*).*—Probably an uncommon resident, but no winter records, and breeding is undocumented. Usually seen in pairs along rocky beaches; 10–20 pairs estimated during May–July 1989 (DWB).

Black-necked Stilt (*Himantopus mexicanus*).—Very common at shal-

low salt ponds in summer. Many seen during May–July 1989—maximum ca 30 together at Bay Pond, 25 May (DWB). Status in winter uncertain as lack of records may be an artifact of sampling. Considered a summer visitor to the northern Bahamas (Brudenell-Bruce 1975), but occurring year-round in the southern islands, although much less numerous there in winter (Buden 1987a). Breeding.—Five nests (three with four eggs, one with three eggs, and one with one cracked and maggot-infested egg), 31 May–2 July 1989 (DWB).

[Greater Flamingo (*Phoenicopterus ruber*).—Extirpated. Last recorded breeding about 1850, at Carmichael Pond (Allen 1956:122, 127). None of the residents of Port Nelson I queried had ever seen flamingos on Rum Cay.]

Greater Yellowlegs (*Tringa melanoleuca*).*—Nonbreeding visitor. Two seen feeding with a flock of Willets on Yard Pond, and one seen at a temporary freshwater pond, ca 0.5 km north of Mermaid Pond, both on 1 June 1989 (DWB).

Lesser Yellowlegs (*T. flavipes*).—Nonbreeding visitor. One specimen collected by the *Albatross* Expedition (Ridgway 1891), undated, but presumably March 1886.

Willet (*Catoptrophorus semipalmatus*).—Common in summer and possibly resident, but no winter records. Breeding unconfirmed, but very probable. Usually seen at salt ponds and on beaches, and as pairs or singles—maximum 23 together at Yard Pond, 1 June 1989, many circling low and calling agitatedly, probably breeding. One male *C. s. semipalmatus* with slightly enlarged testes was collected at Sumner Point by A. Schwartz on 19 June 1966. The Willet is considered resident on other Bahama Islands, though it is less common in winter than in summer (Brudenell-Bruce 1975, Connor and Loftin 1985).

Spotted Sandpiper (*Actitis macularia*).*—Nonbreeding visitor. Two seen at Carmichael Pond during 13–14 May 1985 (A. Sprunt IV).

Ruddy Turnstone (*Arenaria interpres*).*—Nonbreeding visitor. Seen on beaches and at salt ponds occasionally during May–July 1989: one on 29 May, four on 3 June, one on 13 June, and five on 16 June. Doubtless occurring in winter but no records.

Western Sandpiper (*Calidris mauri*).*—Nonbreeding visitor. Six seen at Carmichael Pond during 13–14 May 1985 (A. Sprunt IV).

Short-billed Dowitcher (*Limnodromus griseus*).*—Nonbreeding visitor. One sight record only: ten at Line Pond, 15 June 1989 (DWB).

Laughing Gull (*Larus atricilla*).—Probably an uncommon to locally common summer visitor, possibly resident. "Seen in small numbers," 10 July 1903 (Riley 1905a), and seen regularly at salt ponds and less commonly on beaches in small groups of up to 20 individuals during May–

July 1989 (DWB). Breeding (all records are 1989 [DWB]).—Three nests (one with one nestling, one with three nestlings, one with one nestling and one egg), Shad Pond, 11 June; one downy young at a pond west of Lake George, 25 June; one nest with four empty, probably rat-eaten eggs at a pond southeast of Lake George, 25 June; ca 20 vociferous, apparently territorial birds (but no direct evidence of breeding) at a small pond near Signal Point, 1 July.

Gull-billed Tern (*Sterna nilotica*).—Uncommon to locally common summer visitor, mainly at salt ponds. "About a dozen were found frequenting a small inland lake," 10 July 1903 (Riley 1905a), and others were seen regularly at salt ponds during May–July 1989 (DWB). Breeding (all records are 1989 [DWB]).—Colony, ca 30 adults, six nests (three with three eggs, two with two eggs, one with one egg), small island at western end of Carmichael Pond, 31 May; colony, ca 40 adults, nine nests (four with two eggs, four with one egg, one with three eggs) plus five mobile, downy chicks, all on an exposed bar at a salt pond near the northwestern shore of Lake George, 25 June. The Carmichael Pond colony was revisited on 16 June, but rats had apparently visited earlier as evidenced by broken eggs and the remains (detached wings, heads, and legs) of several species of birds. Only two adult *S. nilotica* were seen then. Stepping stones exposed during the drought provided access to the island.

Royal Tern (*S. maxima*).—Status uncertain, possibly scarce resident. Seen occasionally along beaches in ones or twos during May–July 1989—maximum ten together at Sandy Point, 31 May (DWB). Riley (1905b) included Rum Cay in his list of localities, but I was unable to locate the source of this record in any of the references he mentioned.

Roseate Tern (*S. dougallii*).*—Uncommon summer visitor. Seen occasionally along beaches and at salt ponds in small groups of 5–20 individuals during May–July 1989 (DWB). Breeding.—Colony, ca 20 adults and several nest scrapes with eggs on a small island at the western end of Carmichael Pond, 31 May 1989 (DWB).

Least Tern (*S. antillarum*).—Common summer visitor. Recorded in July 1903 (Riley 1905a), and many seen during May–July 1989 (DWB). Breeding on exposed bars and broad shores of salt ponds (all records are 1989 [DWB]): Colony, ca 50 adults, 22 clutches (16 with two eggs, five with one egg, one with three eggs), salt pans on northern shore of Carmichael Pond, 31 May; colony, ca 50 adults, 19 clutches (11 with two eggs, seven with one egg, one with two eggs and one downy young) on an exposed bar at a salt pond near the northwestern shore of Lake George, 5 June (eight clutches there on 25 June [five with two eggs, three with one egg], but no young seen); colony, ca 15 adults, six clutches (four with

two eggs, two with one egg) on a small island at the western end of Carmichael Pond, 16 June.

Bridled Tern (*S. anaethetus*).*—Probably a regular summer visitor, but very local. Up to 30 adults seen on or near a bare, rocky islet about 200 m off the northern shore near Boat House Rock, May–July 1989 (DWB). No other locality records. Breeding.—Four clutches: one egg and one downy young in two different rocky crevices, and two downy young sheltered beneath two different slabs of rock, 2 July 1989 (DWB).

White-crowned Pigeon (*Columba leucocephala*).*—Probably an uncommon to fairly common resident, but status in winter is uncertain and breeding is undocumented. Small flocks of 2–10 were seen regularly during May–July 1989, usually roosting in the more heavily wooded areas or in flight mainly at dawn and dusk—maximum 12 together roosting in tall trees near a public well, ca 1.5 km north of Port Nelson, 29 June (DWB).

Zenaida Dove (*Zenaida aurita*).—Fairly common resident, most numerous in relatively open scrub, especially along roadsides and near freshwater—maximum 18 together at a bulldozed pit containing freshwater north of Port Nelson, 29 June 1989 (DWB). Breeding.—Two eggs in a roughly cup-shaped nest consisting only of a few loose strands of grasses on the ground in a sparsely vegetated, seasonally flooded salt flat near the northwestern shore of Lake George, 25 June 1989 (DWB).

Mourning Dove (*Z. macroura*).*—Nonbreeding visitor. Fifty seen during 7–9 March 1976 (MHC). The large number then and no other records suggest the birds were in passage.

Common Ground-Dove (*Columbina passerina*).—Fairly common resident in open scrublands and along roadsides, but breeding is unconfirmed. Most numerous in Port Nelson.

Key West Quail-Dove (*Geotrygon chrysia*).*—Scarce resident, but breeding is unconfirmed. I saw *G. chrysia* on only five occasions in six weeks during May–July 1989, all in xeric woodlands or in scrub adjacent to woodlands: one between Adderley's Pond and Lake George on 5 June, three at three different localities 2–4 km north of Port Nelson on 19 and 26 June and 1 July, and one at the blue hole south of Gin Hill on 23 June.

Mangrove Cuckoo (*Coccyzus minor*).—Probably a scarce to uncommon resident; breeding is unconfirmed. Four collected 1–5 March 1886 (Ridgway 1891), two seen during 7–9 March 1976 (MHC), and several seen and heard in scrublands and woodlands occasionally during May–July 1989 (DWB).

Smooth-billed Ani (*Crotophaga ani*).—Uncommon resident throughout, most numerous in the vicinity of Port Nelson. Breeding is uncon-

firmed. Five collected 1–5 March 1886 (Ridgway 1891), seven seen during 7–9 March 1976 (MCH), and groups of two to eight seen occasionally during May–July 1989 (DWB).

Barn Owl (*Tyto alba*).*—Rare resident, but breeding is unconfirmed. I saw one at Hartford Cave on several different occasions during June 1989, and the large number of presumed prey remains on the floor of the cave (mainly *Rattus* bones) suggests long residence there. Another was seen in *Bucida* woods north of Cotton Field Point, 5 July 1989, and one partial skeleton (USNM 612544) was collected at Hartford Cave on 28 May 1989 (DWB).

Antillean Nighthawk (*Chordeiles gundlachii*).*—Common summer visitor. Most numerous along beaches and on sparsely vegetated shores of ponds. Often seen hawking for insects at dawn and dusk—maximum eight together in flight at dusk near Boat House Rock, 6 June 1989 (DWB). Breeding (all records are 1989 [DWB]).—17 clutches (25 May–7 July) on beaches (seven), along roadsides (six), and shorelines of ponds (four); 14 with one egg, two with one flightless young on 12 and 25 June, and one with two eggs on 7 June. The first ten clutches found during 25 May–7 June were eggs only. One of 17 eggs was white without any discernible markings, whereas all the others were mottled, dusty, bluish-gray on grayish-white.

Bahama Woodstar (*Calliphlox evelynae*).—Fairly common resident throughout. Breeding.—Two used nests I found in June 1989 doubtless belonged to this species.

Yellow-bellied Sapsucker (*Sphyrapicus varius*).—Nonbreeding visitor. The only record is one collected on 1 March 1886 (Ridgway 1891), but numerous sets of horizontal holes on many of the larger trees indicate *S. varius* probably occurs regularly in winter and in passage.

Gray Kingbird (*Tyrannus dominicensis*).—Common to locally very common summer resident. I found *T. dominicensis* most numerous in trees along the coast and at the edges of ponds—maximum concentration, 27 counted in 1.5 h covering 3.5 km ($\bar{x}$ = 7.7/km) between Boat House Rock and the beach opposite Gin Hill, 2 July 1989 (24 counted on 29 June); less common inland—one to 14 counted on 26 different censuses over the 6.5 km of road between Port Nelson and the northern coast during May–July 1989 ($\bar{x}$ = 0.9/km). Breeding (all records are 1989 [DWB]).—A pair seen copulating 7 June; seven nests (two with one egg on 15 June and 2 July, one with three eggs on 27 June, one with two eggs on 7 July) and three other nests under construction, 14–16 June. All the nests were in trees bordering beaches and ponds. Seven of ten were in buttonwood (*Conocarpus erectus*), and most were 2–3 m high in branches.

Gray Catbird (*Dumetella carolinensis*).—Nonbreeding visitor. One col-

lected 6 March 1886 (Ridgway 1891); two seen 7–9 March 1976 (MHC); one seen 4 June 1989 (DWB), the latter an unusual summer record.

Northern Mockingbird (*Mimus polyglottos*).*—The only records are one seen on 7 March and two seen on 8 March 1976 (MHC). Short-lived breeding populations possibly occur from time to time, but until there is evidence to the contrary, I consider *M. polyglottos* a nonbreeding visitor to Rum Cay, probably from adjacent islands. The Northern Mockingbird is widespread throughout the Bahamas, and the few Bahaman breeding records span the archipelago (Buden 1988). The abundance of two other species of mimids, *M. gundlachii* and *Margarops fuscatus,* however, may contribute to the lack of a permanent resident population on Rum Cay. I saw no *M. polyglottos* during six weeks on the island, from late May to early July 1989.

Bahama Mockingbird (*M. gundlachii*).—Very common resident in scrublands and woodlands, but seldom seen in the settlement, where *Margarops fuscatus* is abundant. I saw and heard many calling in the topmost branches of trees and bushes during May–July 1989. Many also were seen foraging on the ground chiefly for insects and other arthropods (two were observed extracting snails [*Cerion*] from their shells), fewer gleaning fruits and insects among trees and bushes. Wing-flashing behavior was evident in some, but not so common nor so vigorous as in *M. polyglottos* elsewhere. Breeding.—One female (AS 7257) with a shelled egg in its oviduct, and one in a nest, was collected in coastal scrub between Sumner Point and Port Nelson by A. Schwartz on 18 June 1966. Many used nests of sticks and twigs I found in scrub east of Port Nelson probably belonged to this species.

Pearly-eyed Thrasher (*Margarops fuscatus*).—Very common resident in scrublands and woodlands, and in Port Nelson. The most abundant land bird on the island during summer 1989, maximum of 11 together were seen feeding and/or drinking among the blossoms of a sisal plant (*Agave sisalina*) at the edge of a beach opposite Gin Hill, 29 June, and 36 were counted during a 6.5 km walk between Port Nelson and the northern coast, 06:00–08:00 h, 1 July (DWB). Generally most numerous in or near patches of woodland or in isolated trees with a shady canopy. Mainly arboreal, usually seen in mid-levels of the vegetation, much less frequently terrestrial. Many seen also on porches of guest houses and in open-sided buildings at the Rum Cay Club. Breeding.—One nest of sticks and twigs under construction (adult observed carrying nesting material) on a shelf in a tool shed at the Rum Cay Club, 1 July 1989 (DWB). A nest I found on the porch of one of the guest houses at the Club probably also belonged to this species.

Thick-billed Vireo (*Vireo crassirostris*).—Very common resident, but

breeding is undocumented. Most numerous in dense scrublands and woodlands.

Black-and-white Warbler (*Mniotilta varia*).—Nonbreeding visitor. The only records are two collected during 2–3 March 1886 (Ridgway 1891), and one seen 7–9 March 1976 (MHC). Owing to the paucity and brevity of previous ornithological surveys, the lack of winter records of this and other warbler species should not suggest they are uncommon during winter or in passage.

Northern Parula (*Parula americana*).—Nonbreeding visitor. One collected 2 March 1886 (Ridgway 1891) and two seen during 7–9 March 1976 (MHC).

Yellow Warbler (*Dendroica petechia*).—Common resident, but breeding is undocumented. Most numerous in mangroves, but common also in scrub and wooded areas throughout. Thirty-four specimens were collected 1–6 March 1886 (Ridgway 1891), and over 50 were seen, mainly in mangroves, during 7–9 March 1976 (MHC). To the best of my knowledge, all specimens of *D. petechia* from Rum Cay are the resident "Cuban-Bahaman subspecies," *D. p. gundlachii.*

Cape May Warbler (*D. tigrina*).—Nonbreeding visitor. Five specimens collected 1–6 March 1886 (Ridgway 1891), and one seen during 7–9 March 1976 (MHC).

Yellow-rumped Warbler (*D. coronata*).—Nonbreeding visitor. Two specimens collected 2 and 5 March 1886 (Ridgway 1891).

Yellow-throated Warbler (*D. dominica*).*—Nonbreeding visitor. One seen during 7–9 March 1976 (MHC).

Prairie Warbler (*D. discolor*).—Nonbreeding visitor. Twenty collected 1–6 March 1886 (Ridgway 1891), and six seen during 7–9 March 1976 (MHC).

Palm Warbler (*D. palmarum*).—Nonbreeding visitor. Seventeen collected 1–6 March 1886 (Ridgway 1891) and more than 60 seen during 7–9 March 1976 (MHC). One I saw in coastal scrub near Boat House Rock on 5 and 6 June (presumably the same bird) in an unusual summer record.

American Redstart (*Setophaga ruticilla*).*—Nonbreeding visitor. One netted during 7–9 March 1976 (MHC).

Ovenbird (*Seiurus noveboracensis*).—Nonbreeding visitor. One collected 5 March 1886 (Ridgway 1891).

Common Yellowthroat (*Geothlypis trichas*).—Nonbreeding visitor. Ten collected 2–6 March 1886 (Ridgway 1891), and one male weighing 9.5 g netted during 7–9 March 1976 (MHC).

Bananaquit (*Coereba flaveola*).—Common resident, but breeding is undocumented. Most numerous in scrublands, and frequently seen foraging

TABLE 1

BREEDING LAND BIRDS OF RUM CAY IN DECREASING ORDER OF ABUNDANCE BASED ON GENERAL OBSERVATIONS AND WITH THE NUMBER OF BIRDS SEEN AND HEARD/KM DURING 12 COUNTS COVERING 42 KM

Species	Abundance[a]	Birds/km
Pearly-eyed Thrasher (*Margarops fuscatus*)	VC	3.7
Thick-billed Vireo (*Vireo crassirostris*)	VC	2.1
Bahama Mockingbird (*Mimus gundlachii*)	VC	1.8
Gray Kingbird (*Tyrannus dominicensis*)	C/VC	1.7
Yellow Warbler (*Dendroica petechia*)	C/VC	1.6
Bananaquit (*Coereba flaveola*)	C	1.7
Zenaida Dove (*Zenaida aurita*)	FC	1.3
Common Ground-Dove (*Columbina passerina*)	FC	1.0
Bahama Woodstar (*Calliphlox evelynae*)	FC	1.0
Antillean Nighthawk (*Chordeiles gundlachii*)	FC	0.5
White-crowned Pigeon (*Columba leucocephala*)	UC/FC	0.9
Black-faced Grassquit (*Tiaris bicolor*)	UC/FC	0.7
American Kestrel (*Falco sparverius*)	UC/FC	0.6
Smooth-billed Ani (*Crotophaga ani*)	UC	0.2
Mangrove Cuckoo (*Coccyzus minor*)	S/UC	0.1
Key West Quail-Dove (*Geotrygon chrysia*)	S	0.0
Barn Owl (*Tyto alba*)	R	0.0

[a] VC = very common, C = common, FC = fairly common, UC = uncommon, S = scarce, R = rare; see Methods for additional explanation.

among blossoms of *Tabebuia* in June and July 1989 (DWB). Two males were netted during 7–9 March, both weighing 12.0 g (MHC).

Black-faced Grassquit (*Tiaris bicolor*).—Uncommon to fairly common resident. Most numerous in dense, weedy vegetation along roads and trails, and in grassy, weedy areas (DWB). Seventeen collected 1–6 March 1886 (Ridgway 1891) and 25 seen during 7–9 March 1976 (MHC). Breeding.—One nest with three eggs, ca 1.5 m high in a bush (*Mimosa bahamensis*) near Mermaid Pond, 26 May 1989, and another with two eggs, ca 1 m high in coastal scrub near Liberty Rock, 2 June 1989 (DWB).

Savannah Sparrow (*Passerculus sandwichensis*).—Nonbreeding visitor. One collected 4 March 1886 (Ridgway 1891).

DISCUSSION

Excluding a questionable record of the Greater Scaup and the long extirpated Greater Flamingo, 70 species of birds are known from Rum Cay, a least 38 of which probably breed there, none endemic to the island. Seventeen (45%) of the breeders or probable breeders are land birds (pigeons to passerines, plus one kestrel) (Table 1), 11 are shorebirds (charadri-

iforms), three are herons, two are ducks, and the remaining five include a grebe, tropicbird, osprey, rail, and moorhen. Five other species (Pied-billed Grebe, Double-crested Cormorant, Reddish Egret, Cattle Egret, and Royal Tern) that breed elsewhere in the Bahamas possibly also breed on Rum Cay but are known only from a few records and their status remains uncertain.

The 17 breeding, land bird species on Rum Cay are widely distributed throughout the Bahamas generally. All occur on adjacent San Salvador, a somewhat larger island (156 km^2) but with proportionately much more water surface. Two land birds that breed on San Salvador but not on Rum Cay are the West Indian Red-bellied Woodpecker (the endemic race *Melanerpes superciliaris nyeanus*) and the Northern Mockingbird, the latter recorded on Rum Cay in March 1976, but not before or since.

Among widespread Bahaman species that do not occur on Rum Cay, nor on San Salvador, are La Sagra's Flycatcher (*Myiarchus sagrae*), Blue-gray Gnatcatcher (*Polioptila caerulea*), which is absent from several other islands in the central Bahamas but common in northern and southern islands, Black-whiskered Vireo (*Vireo altiloquus*), Stripe-headed Tanager (*Spindalis zena*), and Greater Antillean Bullfinch (*Loxigilla violacea*). Additionally, the Greater Antillean Pewee (*Contopus caribaeus*), Red-legged Thrush (*Turdus plumbeus*), and Bahama Yellowthroat (*Geothlypis rostrata*), all of which breed on many of the Great Bank and Little Bank islands to the north and west, also are absent from Rum Cay and San Salvador.

The land birds of Rum Cay occur in all terrestrial habitats, but strong habitat preferences are evident in some. The Zenaida Dove and Common Ground-Dove are most numerous in open, scrubby areas and along roadsides, the Antillean Nighthawk occurs mainly in sparsely vegetated areas of sand, gravel, and rock (especially on beaches, roadsides, and shorelines of ponds), the Gray Kingbird occurs mainly in trees on the coast and at the edges of ponds, and the Yellow Warbler is most numerous in mangroves and the immediately adjacent scrub. The two very common mimids, Bahama Mockingbird and Pearly-eyed Thrasher, overlap broadly in habits and habitat, but the mockingbird is much more numerous in sparse, coastal scrub, usually calls from the topmost branches of the taller trees and bushes, and frequently forages on the ground, whereas the thrasher is more numerous in the more heavily wooded areas, frequently calls and forages in mid-levels of the vegetation, and is much more edificarian, being found in and near buildings in Port Nelson and at the Rum Cay Club.

Table 1 lists the 17 breeding land birds of Rum Cay in decreasing order of abundance based on general observations and on 12 different census

counts. The only noteworthy discrepancy between general observations and censuses is the relatively low count for the Antillean Nighthawk. But during the day, it usually is seen only after being flushed from its nest site, and most individuals allow close approach to within ca 2 m before taking flight, hence the relatively low counts.

Summer is a peak breeding season for many Bahama birds (Brudenell-Bruce 1975, Buden 1987b). I found active nests, eggs, and flightless young of 12 species of waterbirds (including the Osprey) and six of the 17 land birds on Rum Cay during 25 May–8 July 1989. The numbers I obtained for Cat Island during 23 May–28 July 1987 are 14 waterbirds and 12 of 24 land birds (Buden 1987b). Among "fairly common" to "very common" species found breeding on Cat Island during summer 1987 but not on Rum Cay during summer 1989 are the Common Ground-Dove, Bahama Mockingbird, and Thick-billed Vireo. Other species occuring on both islands and found breeding on Cat Island but not on Rum Cay during these surveys were White-crowned Pigeon, Smooth-billed Ani, and Yellow Warbler. The relatively few land birds found breeding on Rum Cay during summer 1989 possibly was due to unusually severe drought (see under Study Area). A large toll of nesting birds probably is claimed also by rats and feral cats.

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EFFECT OF LONG DAYS ON MOLT AND AUTUMN MIGRATORY STATE OF SITE-FAITHFUL DARK-EYED JUNCOS HELD AT THEIR WINTER SITES

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Abstract.—Dark-eyed Juncos (*Junco hyemalis*) caught at their regular winter sites and then held outdoors fail to become restless or to fatten in the following autumn. Two alternative explanations for this failure to manifest the autumn physiological migratory state are (1) that the birds' perception of familiar characteristics of the migratory destination suppresses the autumnal state, or (2) that spring and summer daylengths in the winter range are too short to permit birds held there to complete the annual physiological cycle. We caught juncos in winter on their perennial winter home ranges, held them there during spring and summer, and then monitored their restlessness and fattening next autumn. We divided these winter-caught birds into three treatment groups. The first two were alike in being exposed indoors to long days simulating the photoregime of spring and summer on the breeding range. They differed in that we placed one of the two groups outdoors in view of the natural environment for ten days in late summer, just before monitoring began, whereas during those ten days the other group remained indoors and on the local photoregime until monitoring. The third group was held outdoors throughout spring and summer on the natural daylengths of their winter site. We compared these three site-faithful groups with each other and with juncos that we caught on the breeding range in late summer, displaced to the winter range, and monitored alongside the other groups. The summer-caught juncos fattened and became restless. The site-faithful group that remained indoors until monitoring exhibited a slight tendency to do so. The site-faithfuls that were placed outdoors after long days indoors and the site-faithfuls that spent spring-summer outdoors neither fattened nor became restless. Site-faithful groups exposed to artificially long days molted earlier than birds recently caught on the breeding range and also earlier than the site-faithfuls continuously held outdoors. Recently caught birds probably delayed molt because, although they had experienced long summer days, they had also reproduced. Our results indicate that the previously reported suppression of the autumnal migratory state in juncos held outdoors at the destination of the autumn migration is not attributable to the shorter daylengths the birds experience there during spring and summer. They are less helpful on the question of whether the suppression results from recognition of the winter site. *Received 8 Dec. 1988, accepted 16 Nov. 1989.*

Internal timing mechanisms are important for first-time migrants of some species. Such mechanisms apparently maintain the young bird in autumn migratory condition for a period sufficient to allow it to travel to the winter range of its species or population (e.g., Gwinner 1969, 1986; Berthold 1973, 1975; Berthold and Querner 1981; Ketterson and Nolan 1986). Much less is known of the regulation of subsequent migrations,

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including whether experience and learning replace or modify the timing mechanisms that control the migrations of naive individuals (Gwinner 1986; but see Stimmelmayr 1932, Sniegowski et al. 1988).

We repeatedly have found (Ketterson and Nolan 1983, 1987a, 1987b, 1988) that groups of site-faithful Dark-eyed Juncos (*Junco hyemalis*) caught in winter and detained until the following autumn outdoors on or near their perennial winter home ranges at Bloomington, Indiana (39°N, 86°W) failed to show the autumnal physiological evidence of readiness to migrate that is usual in captive birds. Throughout the fall they put on no migratory fat and exhibited little nocturnal restlessness (*Zugunruhe*). In the following spring, both fattening and restlessness were normal for that season, i.e., were at the levels exhibited by juncos not held over summer at their winter sites. In contrast, juncos caught in late summer on their Canadian breeding grounds, transported to Bloomington, and monitored there with the winter-caught site-faithful individuals both fattened and showed *Zugunruhe* in the autumn immediately after their capture (Ketterson and Nolan 1983, 1986). During the following autumn, after a year in captivity, these juncos again fattened and, to a lesser extent than the preceding year, became restless (Ketterson and Nolan 1987a). Finally, the suppression found in winter site-faithful juncos monitored in cages during autumn was also observed when site-faithful juncos were released at the beginning of autumn both at their migratory destinations and north of those destinations. Most of these birds remained where released, although a few returned to their winter home ranges (Ketterson and Nolan 1988). Interestingly, one individual that remained north of its usual winter site after release returned to its perennial site one year later. This, like the spring resumption of fattening and restlessness by birds that were suppressed in autumn, shows that the observed suppression of the migratory state was not permanent.

We attributed (Ketterson and Nolan 1983, 1986, 1987a) the differences between the site-faithful juncos and the Canada-caught juncos to site recognition. The former group had remained at the perennial destination of its autumn migrations—juncos that are site-faithful return at a rate strongly suggesting that all survivors return (Ketterson and Nolan 1983, 1986)—whereas the latter group almost certainly was not familiar with the region where we monitored them. In autumn, the site-faithful birds did not develop readiness to migrate, whereas the birds that were not on their winter home ranges did so (compare Sniegowski et al. 1988).

We recognized, however, another possible explanation for our results. Birds on artificial photoregimes that differ from those they experience in nature sometimes behave abnormally during the remainder of the annual

cycle (Wolfson 1960a, 1960b; Moore et al. 1982; Donham et al. 1983; Farner et al. 1983; Gwinner 1986). Juncos caught and held at their winter sites during the following spring and summer are exposed to shorter days than juncos on the breeding range. Thus, perhaps the site-faithfuls had not been exposed to days long enough to induce the migratory state. This possibility was not precluded by the fact that Canada-caught juncos had fattened and grown restless in autumn after a year's captivity in Bloomington (Ketterson and Nolan 1987a) because their breeding grounds (at 49°N) may have been south of the breeding grounds of the site-faithful juncos (unknown, but juncos breed well beyond 49°N, American Ornithologists' Union 1983). This possibility deserved a direct test. Accordingly, in the experiment reported here we performed photoperiodic manipulations to test the hypothesis that the summer daylengths of Indiana were too brief to elicit normal autumn physiology in site-faithful juncos caught in Indiana in winter but sufficed for juncos caught during summer in Canada at 49°N. Anticipating that longer days might induce fattening and *Zugunruhe,* we also varied the exposure of site-faithful juncos to local cues that might be associated with recognition.

METHODS

We divided subjects into four treatment groups based on differences in their histories in the period between winter 1983–1984 and late August 1984, when we began monitoring *Zugunruhe* and fattening. These differences are described below.

Group 1 (9 males), after capture in winter, was held until 28 March 1984 in large outdoor aviary cages (described in Ketterson and Nolan 1983, 1986). On that date, which is near the mid-point of the junco's spring migration at Bloomington (pers. obs.), the birds were placed together in a windowless compartment about 2 × 2 × 3 m in size. Two fluorescent lights on the ceiling produced 22 lux at 1 m above the floor. One light was turned on before the other to simulate morning civil twilight, and the opposite was done to simulate evening civil twilight (Nautical Almanac 1984). Between 28 March and 26 April the daily light : dark cycle of the room was changed gradually in an effort to subject the birds to the approximate daylengths they would have experienced had they been migrating northward from Bloomington toward latitude 52°N (Fig. 1). Thereafter, from 26 April to 10 August, the photoregime was that of 52°N (Fig. 1; longest day between civil twilights: 21 h 13 min). On 10 August, the birds were removed and taken, in the same building, to a room with windows; there they experienced natural Indiana daylengths. On 20 August, each was placed in a separate opaque bag and taken to its individual registration cage on the roof of the building (the setup and environment are described in Ketterson and Nolan 1983) and thereafter monitored.

Group 2 (9 males) was identical in its history to Group 1, except that on 10 August its members were taken from the artificially lighted compartment and returned to one of the original outdoor aviary cages until 20 August, when they also were put in individual cages on the roof. Thus for 10 days in mid-August these juncos were exposed to normal geophysical and celestial characteristics of the destination of their previous migration(s) and could view

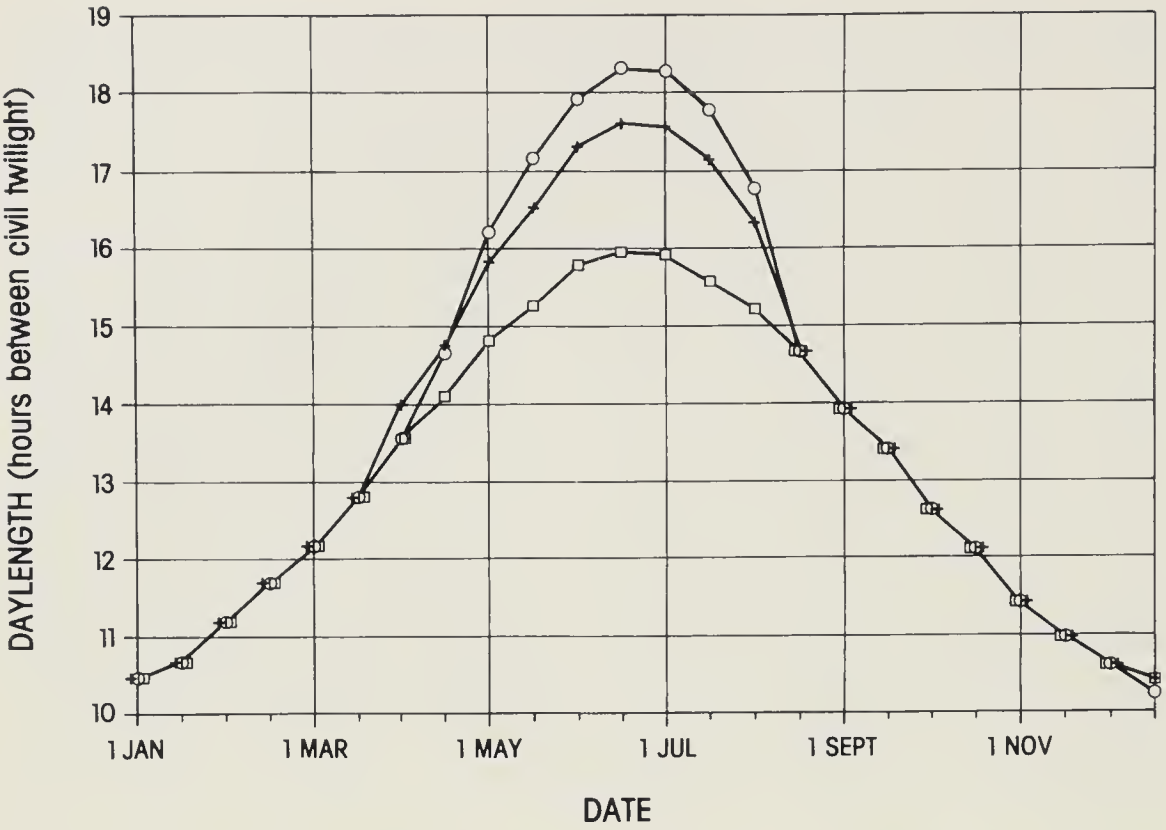

FIG. 1. Daylength according to treatment group. Lower curve depicts annual variation in daylength at Bloomington, Indiana and describes daylength experienced by Group 3 (see text). Upper curve refers to Groups 1 and 2 (see text) which were transferred indoors on 28 March and subjected to increasing daylengths to simulate a journey northward and then a breeding season at 52°N. On 10 August, Groups 1 and 2 were returned to natural Indiana daylengths. The middle curve refers to Group 4 (see text) and describes the daylengths that would be experienced by juncos that wintered near 39°N and then migrated during March to 49°N, the breeding latitude of the Group 4 juncos. Group 4 was transported southward to 39°N or 3 August.

the surroundings of the aviary. Reasons for this 10-day difference in treatment of Groups 1 and 2 will be given below.

Group 3 (9 males) juncos also were caught on winter home ranges near Bloomington where they had lived in at least one previous season and were placed in the large outdoor cages of the aviary. The aviary was 10–20 km from their winter home ranges and 1.5 km from the roof on which they were to be monitored in autumn. They were moved to individual outdoor registration cages on the roof on 20 August. Therefore these birds always experienced the natural Bloomington photoregime (longest day: 15 h 58 min, Fig. 1).

Group 4 (10 males) was caught in Wawa, Ontario (49°N), between 19 July and 1 August. In all probability the birds had bred at Wawa (longest day: 17 h 38 min, Fig. 1). On 2–3 August 1984 they were brought to Bloomington and held outdoors at the aviary until 26 August, when they were put in individual registration cages to be monitored. These Canada-caught birds differed from the winter site-faithful juncos in several ways that made them less than ideal controls, but we saw them as insurance: if they exhibited migratory physiology and all of the site-faithfuls did not, we could eliminate the possibility that some condition of our monitoring had suppressed restlessness and fattening.

The reason for exposing the Group 2 juncos to the outdoor environs of the aviary between 10 August and 20 August, while leaving the Group 1 juncos indoors, was as follows: Juncos housed indoors on long days may have been deprived of outdoor cues necessary to permit them to recognize that they were at their winter site, whereas juncos held outdoors on natural days were not deprived of such possible cues. This would introduce a confounding variable if it turned out that the experiment revealed differences between long-day and short-day juncos. The transfer of Group 2 to the aviary for 10 days was an attempt to expose these birds to outdoor cues and thereby eliminate or minimize the potentially confounding variable—difference in place of confinement—prior to the experiment.

Zugunruhe, molt, and fattening were measured as previously described (Ketterson and Nolan 1983, 1986, 1987a, 1987b). *Zugunruhe* was quantified for each individual by totalling with a microcomputer the number of 30-sec intervals of activity between the hours 21:00–04:30 (its nightly score). We then summed each bird's nightly scores over the full autumn (its seasonal total), counted the nights during which it exhibited activity for at least 30 minutes (its number of active nights), and noted the value of its nightly score on the night when it was most active (its maximum night). Monitoring of *Zugunruhe* began on 20 August (26 August for Group 4) and continued until 1 December, when an unauthorized person released all the birds and terminated the experiment somewhat sooner than we had planned (compare Ketterson and Nolan 1983, 1986, 1987a, 1987b).

Extent of fattening was determined in two ways. First, we computed for each individual the difference between its initial mass in late August and its maximum mass during autumn, as measured in a series of inspections about two weeks apart. This difference we express in absolute terms and also as a percentage of initial mass. Second, at each inspection we classified subjects according to amount of visible subcutaneous fat, employing a previously described scale of 0–5 (Nolan and Ketterson 1983). We have observed a high correlation between this index and fat extractable in the laboratory (Rogers et al., unpubl. data). Molt was monitored at each inspection, using methods previously described (Ketterson and Nolan 1987a).

We employed the Kruskal-Wallis nonparametric ANOVA to test for differences among groups. *A posteriori* multiple comparisons based on Kruskal-Wallis rank sums were performed as described in Sokal and Rohlf (1969). Because the multiple comparisons require equal sample sizes, we randomly eliminated (by assigning numbers and drawing lots) one male from Group 4 for these tests.

RESULTS

Zugunruhe.—In Kruskal-Wallis tests, groups differed in all measures of *Zugunruhe* (Table 1 footnotes). Group 4 was the most active and Group 1 the next most active, while Groups 2 and 3 exhibited almost no activity (Table 1, Fig. 2). In multiple comparisons of seasonal totals and numbers of active nights, Group 4 juncos were significantly more restless than Groups 1, 2 or 3 ($P < 0.05$) which did not differ from one another. For maximum nightly score, Group 4's score was greater than that of Groups 2 and 3 ($P < 0.05$) but not of Group 1 ($P > 0.05$). Group 1 also could not be distinguished from Groups 2 and 3 ($P > 0.05$) and hence was intermediate in maximum nightly score.

Body mass and fat class.—Intergroup differences in gain in mass (Table 2, Fig. 3) were significant (Kruskal-Wallis, $P < 0.05$). Multiple compar-

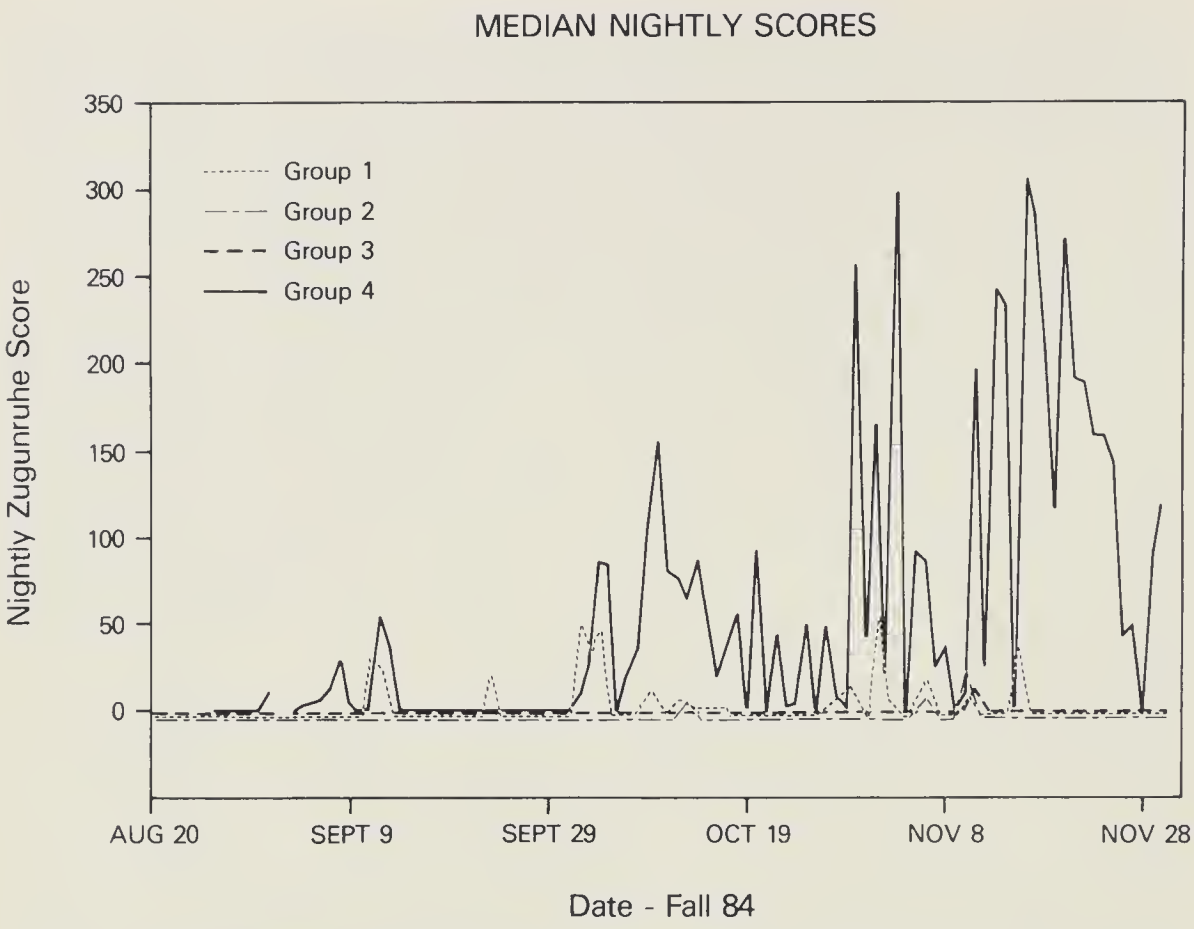

FIG. 2. Median nightly *Zugunruhe* scores according to date for Groups 1–4. The day-lengths experienced by the groups are described in the caption to Fig. 1. Groups differ additionally in that Group 1 remained indoors between 10 and 20 August and was thus given no exposure at this time to the environmental cues being experienced by Groups 2–4.

isons of absolute gain show that Group 4 made significantly greater absolute gains than Groups 1, 2, and 3, which did not differ from one another. In percentage gain (Table 2), Group 4 differed from Groups 2 and 3. Group 1 was intermediate; its gain could not be distinguished from those of Groups 2 and 3.

The median fat class (data not shown) of Groups 1–3 never exceeded 0.5 during the experiment, whereas the median fat class of Group 4 rose from 0.5 on 8 October to 3.0 on 8 November and was 3.5 at the end of the experiment.

Molt.—Although the date of first examination for molt was not identical for all groups, it is clear (Fig.4) that Groups 1 and 2 began to molt earlier than Groups 3 and 4, probably about one month earlier. The conclusion that Group 4 birds molted later than Groups 1 and 2 is supported by further evidence: among 57 free-living adult juncos (including Group 4) that we caught and examined at Wawa during the period when we captured

TABLE 1

AUTUMN *ZUGUNRUHE*[a] OF GROUPS[b] OF DARK-EYED JUNCOS SUBJECTED TO PHOTOPERIODIC AND OTHER TREATMENT DIFFERENCES IN 1984

	Seasonal total[c] median (extremes)	Maximum night[d] median (extremes)	Active nights[e] median (extremes)
Group 1	2154 (39–9015)	190 (17–687)	12 (0–31)
Group 2	204 (14–7578)	49 (5–431)	0 (0–30)
Group 3	308 (17–5332)	50.5 (3–320)	1.5 (0–29)
Group 4	6608 (2386–14,327)	500 (196–757)	27 (16–68)

[a] Perch hops were monitored by microcomputer during 30-sec intervals between 21:00 and 04:30 (900 intervals per night) between 20 August and 1 December 1984. The sum of an individual's nightly scores is its seasonal score; its greatest nightly score is its maximum night; and nights in which its nightly score >60 are its active nights.

[b] See Methods for descriptions of the groups.

[c] Kruskal-Wallis, $H = 14.32$, $P < 0.003$. Pairwise multiple comparisons non-significant except when Group 4 compared to Groups 1, 2, and 3 ($P < 0.05$).

[d] Kruskal-Wallis, $H = 12.07$, $P < 0.001$. Pairwise multiple comparisons non-significant except when Group 4 compared to Groups 2 and 3 ($P < 0.05$).

[e] Kruskal-Wallis, $H = 12.87$, $P < 0.005$. Pairwise multiple comparisons non-significant except when Group 4 compared to Groups 1, 2, and 3 ($P < 0.05$).

Group 4, only one (possibly two) individuals had begun to molt in late July. By that date, all members of Groups 1 and 2 were well advanced in molt.

DISCUSSION

The most striking result of this experiment is the failure of any group of winter-caught site-faithful juncos (Groups 1–3) to become as restless or as fat as recently caught breeders from 49°N (Group 4), regardless of whether the site-faithful juncos had experienced the spring-summer photoregime of 39°N (Group 3) or of 52°N (Groups 1 and 2). These results indicate that exposure to the shorter summer days of the winter site cannot alone explain the suppression of autumn physiology in juncos held over summer at or near their winter sites. Thus, earlier reports of this suppression which were interpreted as possible evidence for recognition of the winter site do not need to be reinterpreted as simply an artifact of photoperiodic treatment. But the results of this experiment add little to answering the question of whether the suppression is properly attributable to recognition. We do not know when recognition, if that is what is responsible, takes place or what cues are required. If recognition can occur as late as late August or September and can take place from a small cage

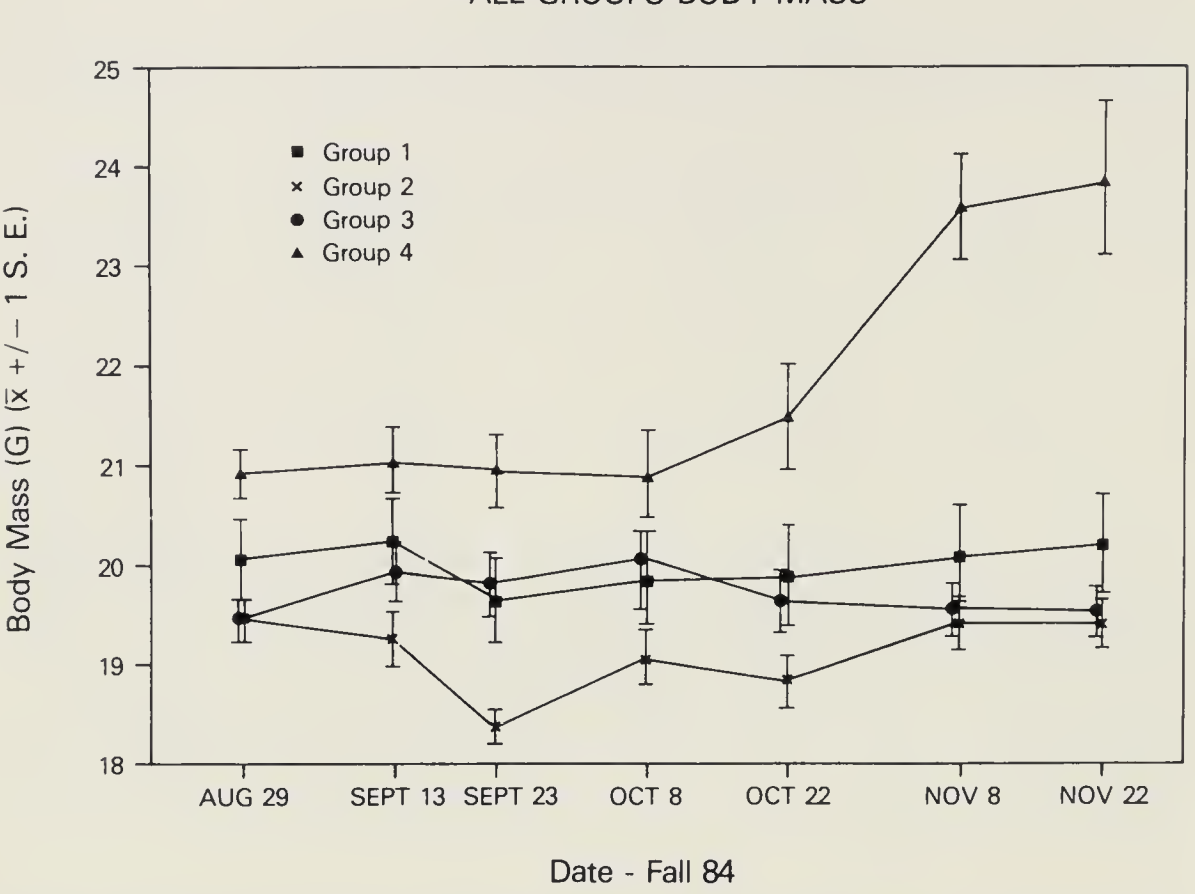

FIG. 3. Mean body mass (±one SE) according to date for Groups 1–4 (see caption to Fig. 2).

TABLE 2

MAXIMUM GAIN[a] IN BODY MASS, AUTUMN 1984, ACCORDING TO GROUP[b]

	Absolute gain (g)[c] mean (extremes)	Gain as % of initial mass[c] mean (extremes)
Group 1	0.90 (−0.5–3.7)	5.0 (−2–19)
Group 2	0.20 (0–0.7)	1.0 (0–4)
Group 3	0.40 (−0.2–1.8)	2.0 (−1–10)
Group 4	2.5 (0.9–8.8)	12.0 (4–44)

[a] For each individual, mass near the beginning of the experiment was subtracted from maximum mass attained thereafter. In a Kruskal-Wallis analysis of variance of absolute change, $H = 17.17$, df = 3, $P < 0.001$. In the same test of percentage change, $H = 16.37$, df = 3, $P < 0.001$.

[b] See Methods for descriptions of the groups.

[c] Multiple pairwise comparisons of groups were non-significant except when Group 4 was compared to Groups 1, 2, and 3 for absolute gain and to Groups 2 and 3 for percentage gain ($P < 0.05$).

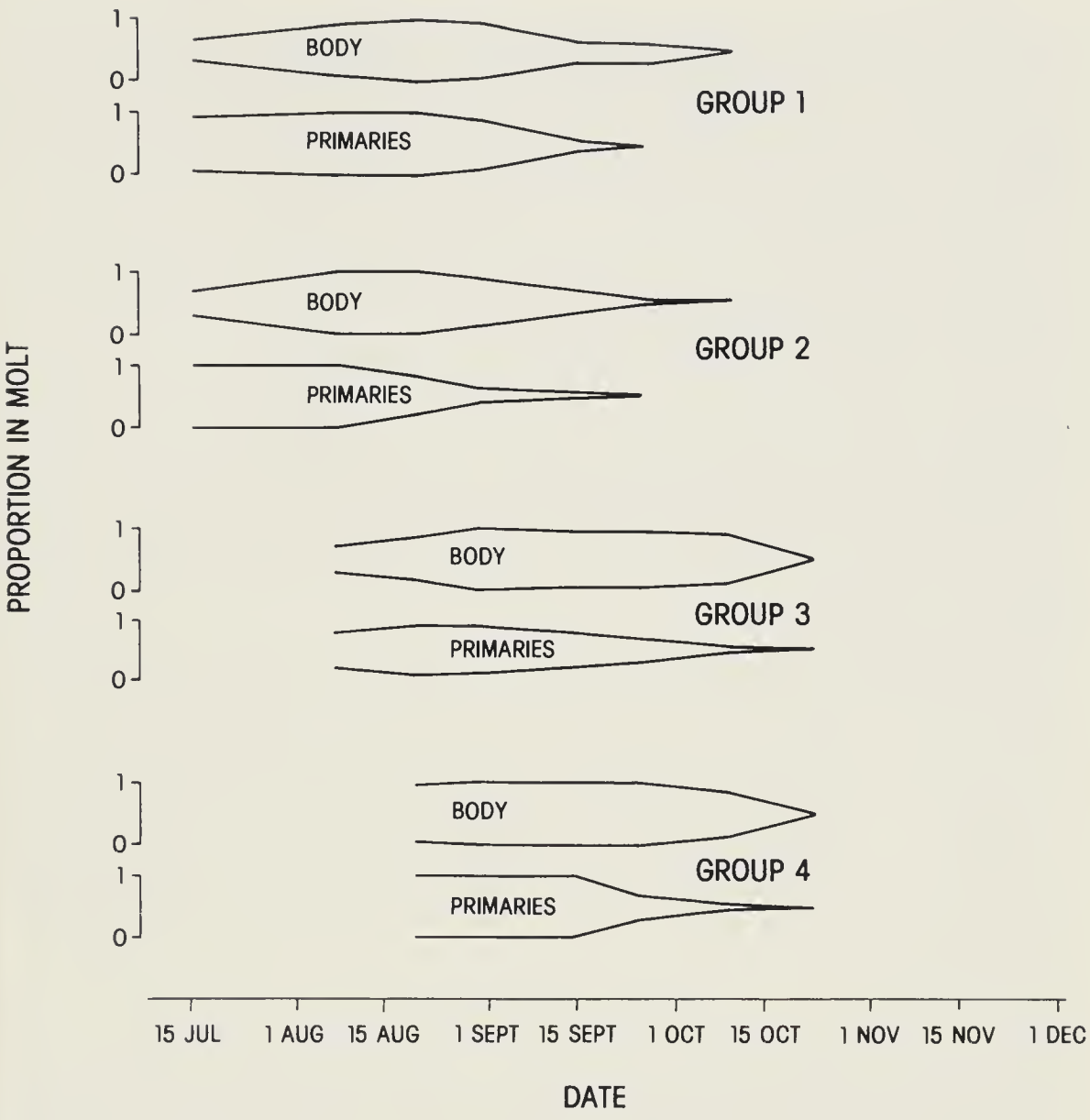

FIG. 4. Proportion in molt according to date for Groups 1–4 (see caption to Fig. 1).

on a roof, then the results of this experiment are consistent with recognition by Groups 1–3. If recognition requires cues not perceivable from the roof, and if we attach importance to the intermediate fattening and restlessness of Group 1, we might conclude that Groups 2 and 3 were suppressed by recognition, while Group 1, which went directly from indoors to a roof, was not fully suppressed. However, none of our experiments (Ketterson and Nolan 1987b, 1988) has provided any strong direct support for recognition.

In molt schedule, Groups 1 and 2 were alike and were much ahead of Groups 3 and 4, which were alike. Photoperiod has been shown to accelerate or retard molt, according to treatment (e.g., Moore et al. 1982),

yet Groups 3 and 4 were on different photoregimes. We doubt that the similarity of Groups 3 and 4 and their difference from Groups 1 and 2 were caused solely by the fact that Groups 1 and 2 spent most of the summer indoors, while Group 3 and 4 were outdoors. A more persuasive explanation of the timing of molt must take into account both the spring-summer photoregimes and the other summer experiences of all groups. Only Group 4 reproduced. Engaging in reproduction in Canada (Group 4) and experiencing short spring and summer days in Indiana (Group 3) apparently had about equal effects in delaying molt.

The fact that postnuptial molt was normal in its extent (i.e., complete), although somewhat differently timed in all site-faithful juncos, also confirms an earlier finding (Ketterson and Nolan 1987a). In the junco, the suppression of fattening and *Zugunruhe* can take place independently of molt. In contrast, in the White-crowned Sparrow (*Zonotrichia leucophrys*) molt is apparently a precondition for autumn fattening (Moore et al. 1982, Farner et al. 1983).

In sum, whatever suppresses normal autumn physiology in site-faithful juncos held at their migratory destination cannot be overridden solely by long summer days. If suppression has nothing to do with daylength but is caused by some other experience or by the absence of an experience, we suggest two experiences that our site-faithful juncos have lacked: none has made the migration northward in the spring preceding monitoring and none has had the opportunity to breed (but see Ketterson and Nolan 1987a).

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NEST-SITE CHARACTERISTICS AFFECTING SUCCESS AND REUSE OF RED-SHOULDERED HAWK NESTS

W. D. Dijak, B. Tannenbaum,[1] and M. A. Parker[2]

Abstract.—Characteristics of nest sites were studied to determine which attributes are related to repeated use of nests and nesting success of Red-shouldered Hawks (*Buteo lineatus*). Nests in large trees with large support branches and surrounded by a dense understory were most likely to fledge at least one bird. Nests built in pin oaks (*Quercus palustris*) had a higher probability of not fledging any young than nests in other species of tree, although 50% of nests were placed in pin oaks. Nests in large trees with a greater number of support branches in an area with a closed canopy were more likely to be used in successive years than nests in other locations. Hawks using old nests may have a higher nesting success rate than those building new nests. *Received 26 June 1989, accepted 20 Jan. 1990.*

Although several studies have investigated and quantified nesting habitat characteristics (Titus and Mosher 1981, Bednarz and Dinsmore 1982, Morris and Lemon 1983), only a few have commented on the relationship between vegetation structure and the success and frequency of reuse of Red-shouldered Hawk (*Buteo lineatus*) nests (Bednarz 1979, Morris et al. 1982). Bednarz (1979) suggested that Red-shouldered Hawks nest in large trees because this may reduce nest predation and damage from wind and rain. Here we quantify the effects of nest-site characteristics on nesting success and reuse of nest sites in a year-round resident population in southeast Missouri.

STUDY AREA AND METHODS

The study was conducted on the Mingo National Wildlife Refuge located on the Mississippi River floodplain in southeast Missouri. The 8770-ha area is primarily composed of lowland hardwood forest (Korte and Fredrickson 1977). In lesser amounts are cypress swamps, upland hardwood forest, cropland, pasture, and moist soil units. Moist soil units are areas that are seasonally flooded to promote the growth of herbaceous plants to be used by waterfowl. Dominant tree species in the lowland forest include pin oak (*Quercus palustris*), overcup oak (*Q. lyrata*), willow oak (*Q. phellos*), sweetgum (*Liquidambar styraciflua*), elm (*Ulmus* spp.), ash (*Fraxinus* spp.), and hickories (*Carya* spp.).

Woodlands were searched systematically for nests during March and April of 1982 and 1983 using the methods of Craighead and Craighead (1956). Vegetation was measured within a 15-m radius circle circumscribing the nest. The species and diameter were recorded for each nest tree. Nest tree height, nest height, and canopy height were measured with a Haga altimeter. The diameter of all trees greater than 5 cm dbh within the 15-m radius circle was

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measured, and the mean was calculated. Basal area was also computed from dbh measurements. Canopy closure was measured with a spherical densiometer. Diameter of nest support branches was directly measured on three nests and optically estimated with binoculars for the remaining nests, using the measured branches as a reference. Nest location was categorized by the placement of nests in tree crotches formed with the trunk or placement in crotches away from the main tree bole. The nest-tree difference was defined as the distance the nest was from the top of the nest tree, which was determined by subtracting the nest height from the nest tree height. The relative nest height is the nest height divided by the nest tree height multiplied by 100. Stem densities (stems/ha) of trees within four diameter size classes are represented by saplings, 5.0–10.2 cm; small trees, 10.3–25.4 cm; trees 25.5–50.8 cm; large trees ≥50.9 cm, and, for all size classes, number of trees.

Nest success was determined for a total of 34 nests in 1982 and 1983. Vegetational characteristics associated with successful nests, which fledged at least one bird, were compared with unsuccessful nest, from which no young were fledged, using the Student *t*-test and discriminant function analysis (Nie et al. 1975). Similar comparisons were made for nests used in two consecutive breeding seasons between 1982 and 1985 versus nests used for only one breeding season. To meet the assumption of normality for discriminant function analysis, canopy closure was transformed by squaring and the number of support branches was transformed with a square-root transformation. Occupancy of a particular nest tree during a given breeding season was determined by direct observation of a nest in use, knowledge that an alternate nest site was in use, or knowledge that the nest was in an obvious location that couldn't have been overlooked during the previous year's nest search.

RESULTS

Nest success.—Of the 34 nests monitored during the 1982 and 1983 breeding seasons, 25 successfully fledged at least one bird. An average of 1.79 young were fledged per breeding pair. Successful nests were in significantly larger diameter nest trees surrounded by smaller diameter trees than were unsuccessful nests (Table 1).

Maximum discrimination between successful and unsuccessful nests was found with nest tree dbh, density of saplings, mean support branch diameter, and relative nest height (canonical correlation coefficient = 0.60, Wilks lambda = 0.644, 4 df, $P < 0.010$). The discriminant function analysis was able to classify correctly 100% of the successful nests and 56% of the unsuccessful nests, for an overall classification of 88% based on these four variables. Each nest was then iteratively excluded from the development of the discriminant function and then classified by it. This gave an unbiased estimation of the error rate (Lachenbruch and Mickey 1968). Through this leave-one-out technique, the discriminant function correctly classified 92% of the successful nests and 56% of the unsuccessful nests for an overall classification of 82%.

Ten different tree species were used as nest trees (Table 2). Although pin oak was the most frequently used, it had a significantly higher rate of nest failures (89%) than the other species combined ($\chi^2 = 6.465$, df = 1, $P = 0.013$, corrected for continuity).

TABLE 1

COMPARISON OF NEST-SITE VARIABLES FOR SUCCESSFUL AND UNSUCCESSFUL RED-SHOULDERED HAWK NESTS

Variable	Successful nests (N = 25)		Unsuccessful nests (N = 9)		*P*-value[a]
	Mean	(±SD)	Mean	(±SD)	
Nest tree height (m)	27.8	(3.3)	29.3	(2.5)	0.236
Nest tree dbh (cm)	64.1	(12.0)	53.4	(14.9)	0.038
Canopy closure (%)	90.2	(10.7)	93.9	(8.5)	0.358
Canopy height (m)	22.3	(4.5)	24.1	(3.7)	0.282
Mean tree dbh (cm)	16.4	(3.1)	21.1	(4.1)	0.001[b]
Basal area (m^2/ha)	25.4	(10.2)	33.5	(11.6)	0.056
Branch diameter (cm)	24.5	(5.2)	20.2	(6.6)	0.057
Support branches (n)	2.4	(0.6)	2.4	(0.5)	0.984
Nest-tree difference (m)	10.5	(3.2)	12.3	(2.0)	0.135
Nest height (m)	17.3	(2.9)	17.0	(1.6)	0.778
Relative nest height (%)	62.5	(9.1)	58.2	(4.5)	0.079
Saplings (stems/ha)	361.6	(196.8)	243.6	(143.6)	0.111
Small trees (stems/ha)	250.1	(126.3)	207.4	(53.9)	0.179
Trees (stems/ha)	103.5	(55.6)	136.6	(51.5)	0.128
Large trees (stems/ha)	26.6	(20.5)	40.7	(32.0)	0.135
Number trees (stems/ha)	741.9	(277.1)	628.7	(212.9)	0.276

[a] For comparison of successful and unsuccessful nests by *t*-test.
[b] Means significantly different ($P < 0.05$) when adjusted for experimentwide error for all 16 comparisons.

Successive use of nest.—Twenty-six nests were examined in successive breeding seasons from 1982 until 1985 to determine if they were reused. Nine of the 26 nests were used in at least two consecutive breeding seasons. These nest were located in significantly taller nest trees (Table 3) and in

TABLE 2

NEST-TREE SPECIES OF SUCCESSFUL AND UNSUCCESSFUL RED-SHOULDERED HAWK NESTS

Species	Successful nests (N = 25)	Unsuccessful nests (N = 9)
American sycamore (*Platanus occidentalis*)	2	1
Pin oak (*Quercus palustris*)	8	8
White oak (*Quercus alba*)	2	
Willow oak (*Quercus phellos*)	3	
Swamp white oak (*Quercus bicolor*)	1	
Overcup oak (*Quercus lyrata*)	2	
Sweetgum (*Liquidambar styraciflua*)	3	
Red maple (*Acer rubrum*)	1	
Eastern cottonwood (*Populus deltoides*)	1	
Dead tree	2	

TABLE 3
COMPARISON OF NEST-SITE VARIABLES FOR REUSED NESTS AND NESTS USED ONCE

Variable	Nests used once (N = 17)		Nests reused (N = 9)		*P*-value[a]
	Mean	(±SD)	Mean	(±SD)	
Nest tree height (m)	27.1	(3.4)	29.9	(2.1)	0.036
Nest tree dbh (cm)	61.1	(13.2)	63.4	(16.2)	0.690
Canopy closure (%)	87.2	(10.9)	98.1	(2.0)	0.001
Canopy height (m)	21.8	(5.2)	23.0	(2.8)	0.519
Mean tree dbh (cm)	17.6	(3.6)	18.0	(2.8)	0.773
Basal area (m^2/ha)	31.2	(10.9)	26.4	(10.7)	0.295
Branch diameter (cm)	22.2	(6.9)	24.3	(4.9)	0.429
Support branches (n)	2.3	(0.5)	2.7	(0.9)	0.256
Nest tree difference (m)	10.6	(3.5)	12.2	(3.4)	0.277
Nest height (m)	16.5	(2.0)	17.7	(3.3)	0.265
Relative nest height (%)	61.5	(8.9)	59.2	(10.5)	0.567
Saplings (stems/ha)	380.3	(226.6)	275.0	(111.6)	0.126
Small trees (stems/ha)	259.6	(130.6)	224.7	82.6)	0.476
Trees (stem/ha)	116.4	(54.9)	111.5	(56.7)	0.832
Large trees (stems/ha)	34.9	(23.9)	29.8	(21.7)	0.601
Number trees (stems/ha)	791.4	(310.4)	641.3	(165.8)	0.192

[a] Comparison by *t*-test.
[b] Means significantly different ($P < 0.05$) when adjusted for experimentwide error for all 16 comparisons.

areas having a higher percentage canopy closure than nests not used consecutively. Successively used nests had a mean canopy closure of 98.1%, whereas nests used for only one season had a mean canopy closure of 87.2%. The discriminant function separating nests used for one breeding season and nests used successively was positively weighted by both canopy closure and number of support branches (canonical correlation coefficient = 0.59, Wilks lambda = 0.655, df = 2, $P < 0.008$). The discriminant function correctly classified 67% of the nests used in consecutive breeding seasons and 94% of those used for one breeding for an overall classification of 85%. Through the leave-one-out method, the discriminant function analysis correctly classified 67% of the nests used in consecutive breeding seasons and 76% of the nests used for only one season. The overall rate of classification was 73%. Although eight of nine reused nests were successful their first season, the number of successful nests was not significantly greater than nests used for only one season ($\chi^2 = 0.32$, df = 1, $P = 0.59$, corrected for continuity).

DISCUSSION

Large diameter support branches were found to be associated with Red-shouldered Hawk nests by Bednarz and Dinsmore (1982). In our study,

successful nests were most often in crotches of large-diameter trees having large diameter support branches. Large tree diameter and support branch diameter probably increase nest stability in high winds. Many of the nest failures occurred by nest abandonment early in the nesting chronology. Instability of nest locations may not have become apparent until nests were constructed. One nest was blown completely out of the tree during high winds.

The higher success rate of Red-shouldered Hawk nests surrounded by high densities of small-diameter trees may be partly attributed to the additional protection from high winds. Nest visibility is also reduced decreasing the likelihood of aerial predation and disturbance from the ground.

Relative nest height reflects the location of the nest within the tree crown. Successful nests tended to be placed proportionally higher within the tree crown than unsuccessful nests.

Although Bent (1937) and Bednarz (1979) concluded that nest tree species was a relatively unimportant factor to nest site selection, it was an important factor to nest success in our study. Nests in pin oaks were much more likely to fail than nests in other trees. Bent (1937) reported that most nests were placed in the main fork of the trunk and two or more branches at an acute angle and that horizontal branches against the trunk or in the forks of branches were rarely used. Similarly in our study, only four of the 34 nests we examined were in forks of branches away from the trunk, although all were successful. Remaining nests were in main forks of the trunk and side branches. However, because pin oak has a strongly excurrent growth form (Fowells 1965) with nearly horizontal branching, it may not provide ideal branching structure for nest placement.

Morris et al. (1982) found no relationship between structural characteristics of nest sites and nest success in their study area in Quebec. They also did not believe that there was any shortage of adequate nesting sites at the time of their study. However, in years of high breeding pair densities, ideal nest sites may be in short supply in areas where nesting sites are limited. Henny et al. (1973) concluded that Red-shouldered Hawk nesting success was inversely proportional to the number of breeding pairs present at Patuxent Wildlife Research Center.

Bent (1937) was impressed with the constancy with which each pair, or its successors, clung to its chosen territory. As breeding pair densities increase and new pairs try to establish territories among the mosaic of established territories, they may have to accept less than prime nest sites, thus reducing the probability of a successful nesting.

Nests that are used successively may reflect sites that have physical

attributes that improve the probability of successful nesting. Although 89% of the nests used in consecutive years were successful compared to 71% for nests used for only one season, the success rates were not significantly different. This may be due to small sample size or a small value in one cell of the Chi-square test.

In comparing Red-shouldered Hawk nest sites to randomly selected plots, Tannenbaum et al. (unpubl. data) found nest tree height to be an important characteristic. In our study, only nest trees 26 m or taller were used in consecutive years. The taller nest trees associated with successively used nests reflect the overall tree size necessary to provide adequately stout branches at an advantageous height for nesting. Management to enhance lowland hardwood forests for Red-shouldered Hawk nesting habitat should provide for large-diameter trees with many large diameter branches in areas with a high percentage canopy closure and high densities of small-diameter trees.

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STOPOVER ON A GULF COAST BARRIER ISLAND BY SPRING TRANS-GULF MIGRANTS

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ABSTRACT.—Neotropical passerine migrants were studied when they stopped on a barrier island along the coast of Mississippi following spring trans-Gulf migration. Peak numbers of migrants occurred from mid-April through early May 1987. Males of several species arrived earlier than females, suggesting that females initiated spring migration later. When migrants stopped on Horn Island they used Scrub/Shrub, Pine Forest, and Relic Dune habitats more than expected if they were distributed independently of habitat type. Scrub/Shrub habitat was characterized by the greatest number of species, the highest species diversity, and the largest number of individuals. Migrants foraged alone or in small flocks usually composed of a single species. Birds were preyed upon during stopover, suffered starvation when they stopped in an energetically stressed condition, and succumbed to adverse weather during migration. Stopover areas must be viewed as important links in species' annual cycle if the conservation of migratory passerines is to be successful. *Received 30 Aug. 1989, accepted 1 Dec. 1989.*

Decline in populations of Neotropical passerine migrants is a serious conservation problem (Keast and Morton 1980, Rappole et al. 1983); one that may be linked to habitat loss on the wintering grounds (e.g., Robbins et al. 1989) or fragmentation of forested breeding habitat (e.g., Wilcove 1988, Holmes and Sherry 1988). A third factor that affects migrant populations is the availability of suitable en route habitat, where the energy reserves critical to a successful migration can be replenished rapidly and safely. When neotropical migrants stopover after crossing the Gulf of Mexico (Rappole and Warner 1976, Moore and Kerlinger 1987), the woodlands and wooded barrier islands along the northern Gulf coast provide the last possible foraging opportunity before fall migrants cross the Gulf of Mexico and the first potential landfall for birds returning north in spring. They provide a place to deposit energy reserves before fall migrants undertake a nonstop flight (18–24 h) of >1000 km, and they give spring migrants a place to rest and replenish reserves following trans-Gulf flight.

We first describe briefly the pattern of arrival of neotropical passerine migrants that stop during spring migration on Horn Island, a barrier island along the northern coast of the Gulf of Mexico. Because sex-related differences in time-of-arrival on the breeding grounds are widespread among

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passerine migrants (e.g., Francis and Cooke 1986), we also examine arrival dates of males and females for several species. Second, we describe habitat use by spring migrants on Horn Island. The suitability of stopover habitat influences the rate of which migrants replenish energy reserves, how long they interrupt migration to stay at a site, opportunities to choose suitable sites later in migration (see Piersma 1987), and ultimately the migrant's survival and reproductive success. We follow Hutto's (1985) definition of habitat as ". . . a spatially contiguous type that appears more or less homogeneous throughout and is physiognomically distinctive from other such types." Third, we report on the flocking behavior of migrants during stopovers on Horn Island following trans-Gulf migration. Sociality may provide both feeding and anti-predator advantages for migratory birds (Morse 1977, Pulliam and Millikan 1982) during stopover in unfamiliar habitat. Fourth, we identify sources of mortality associated with trans-Gulf migration. Adverse weather is a major cause of mortality (e.g., Ligon 1968, Whitmore et al. 1977) and small passerines are at risk when crossing water barriers (e.g., Saunders 1907, Cooke in Chapman 1907, Paynter 1953, Bullis 1954, James 1956). Migrants are also vulnerable to predation, especially when energy considerations assume priority (e.g., Metcalfe and Furness 1984, Kerlinger 1989, Lindstrom 1989).

STUDY AREA AND METHODS

Horn Island is one of more than 50 barrier islands that border the northern Gulf of Mexico (Fig. 1). As a federally designated wilderness area in the Gulf Islands National Seashore, it is the least disturbed barrier island in the Gulf of Mexico. Located approximately 14 km from the Mississippi coast, the 1400-ha island ranges in width from several hundred meters to just over 1 km and is 22 km long. A variety of aquatic and terrestrial habitats include 60 permanent ponds and lagoons and uplands ranging from intertidal sand flats to vegetated dunes > 10 m in elevation (Eleuterius 1979). We identified five plant habitats during this study. The percent of the island occupied by a particular habitat, after excluding barren sand and open water (25% of total island area), is noted parenthetically in the following descriptions.

Primary Dune (14.4%) borders the inter-tidal zone on both sides of the island and is dominated by *Uniola paniculata* and *Andropogon maritimus. Marsh/Meadow* (28.9%) habitat is dominated by expansive stands of *Juncus roemerianus, Spartina alterniflora,* and *S. patens* in tidal flood areas, or *Fuirena scirpoidea, Panicum repens,* and *Andropogon virginicus* in fresh water areas, with occasional shrubs (*Baccharis halimifolia* and *Myrica cerifera*) and living and dead slash pines (*Pinus elliotti*) along the edges. *Scrub/Shrub* (14%) consists of shrub thickets, which range to 5 m in height, that are dominated by *B. halimifolia* and *M. cerifera* on wetter sites and by *Ilex vomitoria,* dwarf live oak (*Quercus geminata*), and *Serenoa repens* on drier sites. *Relic Dune* (28.8%) refers to high, dry relic dune ridges characterized by sparse low shrubs, *Solidago pauciflosculosa, Ceratiola ericoides,* the rock-rose *Helianthemum arenicola, Opuntia* cactus, and a few emergent slash pine and dwarf live oak. *Forest* (13.9%) habitat consists of a slash pine canopy, with small numbers of *Quercus geminata* and an understory that ranges from open on drier sites to dense thickets of *Myrica, Baccharis,* and *Ilex* on wetter sites.

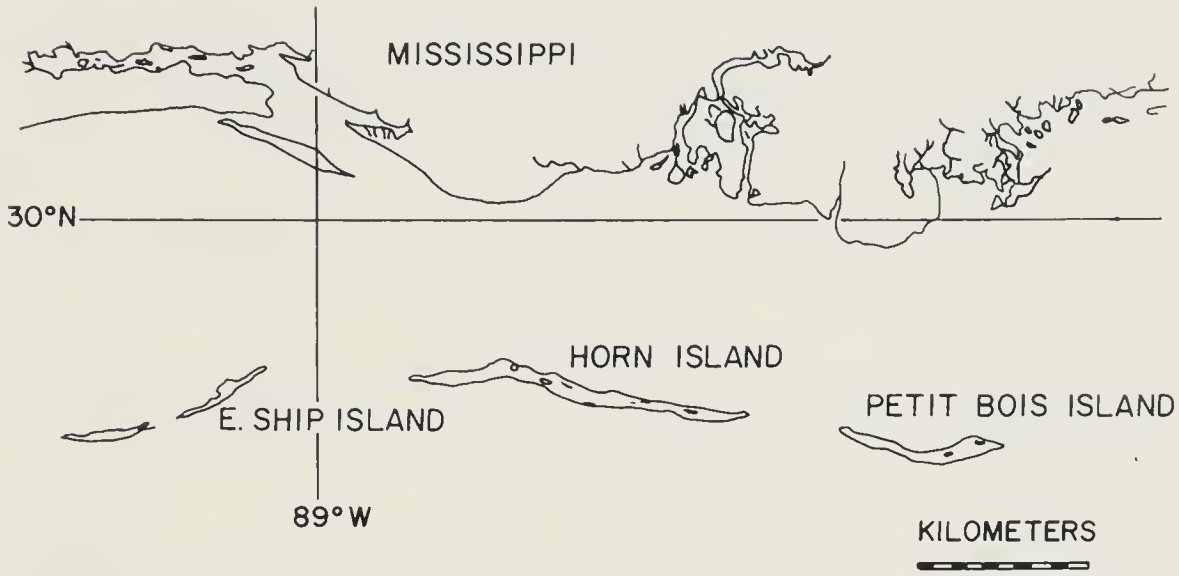

FIG. 1. Map showing barrier islands along the northern coast of the Gulf of Mexico. Sampling sites are located on Horn Island.

The bird species observed in this study were intercontinental migrants that winter in the Caribbean basin, Central America, and South America and breed in temperate North America. All but Ruby-throated Hummingbirds (*Archilochus colubris*) and Yellow-billed Cuckoos (*Coccyzus americanus*) were passerines. Point counts were used to estimate the number of species stopping on the island and to provide an index of abundance. No effort was made to estimate the absolute density of the migrants that stopover on the island. Sampling points were established at 50-m intervals along three transects that passed through each of the five habitats. A point within each habitat type along the three transects was selected randomly (three points per habitat) and counts conducted twice daily in each habitat type: once in the morning (07:30–10:00 CST) and once in the afternoon (15:30–18:00 CST). The order of daily visitation to habitat types was randomized. At each stop, the observer recorded all birds seen within that habitat type during a 10-min period, although only individuals perched, foraging, or displaying aggressive behavior were included in the analysis of habitat use. Association with a flock while foraging was noted as well as whether the flock was mixed or homospecific. Observations were made daily 21 March to 9 May 1987 in Primary Dune, Marsh/Meadow, Forest, and Scrub/Shrub habitats. Relic Dune was added as a habitat type on 10 April.

RESULTS

Pattern of arrival.—Although the number of species stopping on Horn Island following trans-Gulf migration varied daily, species numbers increased in mid-April and averaged about 25 spp./day until the end of the study. The cumulative number of species increased rapidly during mid-April, after which the rate slowed. The number of individuals that arrived on the island also varied from day to day, although peak numbers were evident during late April through the second week in May.

Males appeared earlier than females among the eight species for which we have adequate samples (Table 1). The arrival of the first female was

TABLE 1

ARRIVAL OF MALES (M) AND FEMALES (F) ON HORN ISLAND DURING SPRING 1987 FOR 8 SPECIES OF SEXUALLY DIMORPHIC TRANS-GULF MIGRANTS

Species[a]	First dates by sex		M:F 1st 10 birds[a]	N[b] (% M)
Black-and-white Warbler[c]	M—3/24	F—3/24	19:2	57 (61)
Hooded Warbler	M—3/24	F—4/02	10:0	98 (67)
Prothonotary Warbler	M—3/25	F—3/28	15:1	110 (73)
Ruby-throated Hummingbird	M—3/26	F—3/31	18:4	224 (55)
Summer Tanager	M—3/27	F—4/08	14:6	128 (66)
Orchard Oriole	M—3/29	F—4/12	10:0	185 (54)
Indigo Bunting	M—4/12	F—4/14	11:1	160 (70)
Rose-breasted Grosbeak	M—4/13	F—4/18	16:1	92 (74)

[a] The number of males may have exceeded 10 because several individuals were usually observed on the day that the cumulative number of birds reached 10.

[b] Sample sizes greater than those given in Table 2 because (1) only individuals observed feeding or perched are counted in Table 2 and (2) individuals observed before 10 April are not included in Table 2.

[c] Scientific names given in Table 2.

at least two days later than the first male in seven of eight species. The overall sex ratio for all eight species was skewed toward males. Females may be under-sampled because of differential detectability, although males and females of seven species for which we have adequate samples (Ruby-throated Hummingbird, Scarlet and Summer tanagers [scientific names not given in the text are listed in Table 2], Black-and-white Warbler, Prothonotary Warbler, Orchard Oriole, and Indigo Bunting) used similar habitats on the island (χ^2 analyses, $P > 0.05$).

Habitat use.—Our analysis of habitat use was divided into two parts based on the pattern of trans-Gulf migration during spring 1987. Before 10 April few migrants stopped on the island (N = 135 or 9% of the total number of migrants observed during this study). Most trans-Gulf migration occurred after 10 April, which coincided with the addition of Relic Dune as a fifth habitat type. Trans-Gulf migrants were distributed unequally among habitats before and after 10 April, although sample sizes were not sufficient to permit species comparisons prior to 10 April. Nevertheless, a one-way ANOVA of individuals of all species indicated significant variation in the mean number of detections during the early period of trans-Gulf migration, and a Tukey's multiple range test (Zar 1984) separated Scrub/Shrub habitat from the other types. A second ANOVA (after 10 April) yielded comparable results. Whereas migrants used Primary Dune and Marsh/Meadow habitats significantly less often than the other habitat types, Tukey's test failed to distinguish between use of Forest and Relic Dune and between Relic Dune and Scrub/Shrub habitats after

TABLE 2

THE PERCENTAGE OF OBSERVATIONS IN EACH OF FIVE HABITAT TYPES BY SPRING TRANS-GULF MIGRANTS THAT STOPPED ON HORN ISLAND BETWEEN 10 APRIL AND 13 MAY 1987. PERCENT OCCURRENCE AMONG FIVE HABITAT TYPES DEVIATES SIGNIFICANTLY FROM EXPECTED FOR EACH SPECIES ACCORDING TO CHI-SQUARE ANALYSES

Species[a]	Scrub/shrub	Primary dune	Marsh/ Meadow	Pine forest	Relic dune	Total N
Yellow-billed Cuckoo *Coccyzus americanus*	47%	—	—	20%	33%	45
Ruby-throated Hummingbird *Archilochus colubris*	47	1	21	5	26	128
Great-crested Flycatcher *Myiarchus crinitus*	46	—	2	48	4	84
Eastern Kingbird *Tyrannus tyrannus*	15	11	56	10	7	174
Veery *Catharus fuscescens*	49	—	—	43	8	43
Swainson's Thrush *C. ustulatus*	46	2	—	46	6	58
Wood Thrush *Hylocichla mustelina*	60	—	—	32	8	25
White-eyed Vireo *Vireo griseus*	77	—	—	14	9	49
Red-eyed Vireo *V. olivaceus*	51	—	1	34	13	119
Tennessee Warbler *Vermivora peregrina*	76	—	—	2	22	55
Yellow Warbler *Dendroica petechia*	41	—	—	7	52	39
Black-and-white Warbler *Mniotitla varia*	81	—	—	13	6	31
Prothonotary Warbler *Protonotaria citrea*	76	—	—	4	20	45
Hooded Warbler *Wilsonia citrina*	77	—	—	19	4	37
Summer Tanager *Piranga rubra*	45	—	9	34	13	65
Scarlet Tanager *P. olivacea*	40	—	15	29	16	75
Rose-breasted Grosbeak *Pheucticus ludovicianus*	44	—	3	31	23	39
Blue Grosbeak *Guiraca caerulea*	15	2	7	15	61	47
Indigo Bunting *Passerina cyanea*	26	—	1	24	49	126
Orchard Oriole *Icterus spurius*	43	—	22	7	28	106
% Area occupied by each habitat type	14%	14.4	28.9	13.9	28.8	100
Total individuals[b]	609 (682)	25 (26)	177 (181)	290 (309)	289 (301)	1390 (1499)
Total species[b]	20 (43)	4 (4)	10 (13)	20 (36)	20 (28)	20 (46)

[a] Species for which fewer than 25 individuals were sighted are not included in habitat breakdown.
[b] Total number of individuals and number of species, regardless of sample size, are noted parenthetically.

TABLE 3

RESULTS OF SINGLE FACTOR ANOVA FOR THE DISTRIBUTION OF NEOTROPICAL MIGRANTS PRIOR TO 10 APRIL AND THE PEAK OF SPRING TRANS-GULF MIGRATION (FOUR HABITAT TYPES) AND AFTER 10 APRIL (FIVE HABITAT TYPES) ON HORN ISLAND, 1987

Source of variation	SS	df	MS	*F*
<10 April				
Total	3771.86	27		
Between groups	2361.29	3	787.10	13.39
Within groups	1410.57	24	58.77	$P < 0.001$
>10 April				
Total	37,625.32	80		
Between groups	15,025.28	4	3756.32	11.30
Within groups	22,600.03	76	332.35	$P < 0.001$

10 April (Table 3). Chi-square analysis of the frequency of occurrence of all individuals after 10 April leads to a similar conclusion: Scrub/Shrub, Forest, and Relic Dune were used more by migrants than Primary Dune and Marsh/Meadow. A greater number of species (Table 2) was recorded for the three former habitats. Scrub/Shrub habitat, which represented 14% of available habitat (16% after excluding Primary Dune), was characterized by the greatest number of species, the highest species diversity, and the largest number of individuals (Table 2). More than twice the number of individuals (N = 682) were seen in Scrub/Shrub than any other habitat, and three times more than the number expected if migrants are distributed independent of habitat type. Of the 46 species observed in the study, 94% were seen in Scrub/Shrub, 78% in Forest, 60% in Relic Dune, and only 37% were seen in Marsh/Meadow and Primary Dune. Only six or seven species should be found in Scrub/Shrub habitat if they are distributed independently of habitat type.

Where sample sizes permit analysis, species-specific habitat use patterns are evident (Table 2). Eastern Kingbirds, for example, were the only migrants to use Primary Dune during stopover and one of a few species to use Marsh/Meadow habitat, where 56% were recorded. Whereas migrants were observed in Relic Dune (Table 2), only Yellow Warblers, Blue Grosbeaks, and Indigo Buntings occupied this habitat more frequently than expected if they were distributed independently of habitat type. More than 75% of the sightings of Black-and-white, Hooded, Tennessee, and Prothonotary warblers and of White-eyed Vireos were in Scrub/Shrub

habitat. Several other species were found in Scrub/Shrub habitat more often than any of the other four habitat types (Table 2).

Contingency analysis indicates that the distribution of individual migrants differs between morning and afternoon samples, whether Primary Dune habitat was included or not ($\chi^2 = 76$, $P < 0.001$; $\chi^2 = 67$, $P < 0.001$, respectively). The number of migrants in Scrub/Shrub, the habitat used most often, was less than expected in the afternoon, yet more than expected in the morning when over 50% of all migrants were detected there. The distribution of species among the five habitat types did not differ between morning and afternoon samples.

Flocking.—During "fallouts," when large numbers of migrants landed on the island over a short period of time, birds moved quickly from tree-top to tree-top or shrub to shrub among habitats, often in loose mixed-species flocks, giving the impression that they were assessing habitats prior to making a choice. There did not appear to be a directional bias to these movements. Movement among habitats declined sharply within one hour of a fallout.

Once migrants "settled" in a habitat, they often foraged alone. Flocks were small and usually were composed of a single species (Table 4). Tennessee Warblers, Indigo Buntings, and Orchard Orioles, which rarely foraged alone (i.e., less than 25% of the observations), were invariably associated with homospecific groups. Rose-breasted Grosbeaks and Swainson's Thrushes were always observed in homospecific groups when flocked. Although both tanager species were observed more often foraging alone, they also formed homospecific groups. The only migrants that occurred in mixed-species flocks more often than homogeneous groups were Black-and-white Warblers and White-eyed Vireos. Red-eyed Vireos, on the other hand, formed single-species flocks, and the majority of those groups consisted of two individuals.

Groups of two were common among several other species during stopovers on Horn Island (Table 4). Among single-species flocks of sexually dimorphic species, heterosexual pairs occurred no more often than expected on the basis of the number of males and females observed ($P > 0.05$). Other single-species groups were seldom larger than three or four individuals (see Table 4) and usually consisted of both sexes. Even among Orchard Orioles and Indigo Buntings, average flock size was less than five.

Source of mortality.—We identified three sources of mortality associated with spring trans-Gulf migration and stopover on Horn Island: (1) death during a trans-Gulf flight, (2) starvation during stopover following trans-Gulf flight, and (3) predation by raptors. The remains of 66 indi-

TABLE 4

FLOCKING TENDENCY (MIXED- AND SINGLE-SPECIES) AMONG NEOTROPICAL MIGRANTS DURING STOPOVER ON HORN ISLAND FOLLOWING TRANS-GULF MIGRATION IN SPRING 1987. AVERAGE SIZE OF SINGLE-SPECIES FLOCKS IS GIVEN FOR SEVERAL SPECIES

Species	N[a]	% of N alone	Single-species flocks			
			%[b]	No. groups[c]	Ave. size	Pairs[d]
Yellow-billed Cuckoo	39	82%	86%	3		3
Veery	40	75	80	3		1
Swainson's Thrush	55	56	100	10	2.4	7
Wood Thrush	25	80	80	2		2
White-eyed Vireo	46	48	25	3		3
Red-eyed Vireo	111	52	72	14	2.6	8
Tennessee Warbler	52	15	70	9	3.4	0
Yellow Warbler	33	48	76	6	2.2	5 (2)
Black-and-white Warbler	26	54	17	4		1 (1)
Prothonotary Warbler	43	33	55	4		0
Hooded Warbler	37	38	52	3		0
Summer Tanager	64	58	81	8	2.8	4 (3)
Scarlet Tanager	70	66	83	9	2.2	7 (5)
Blue Grosbeak	47	62	72	4		1
Rose-breasted Grosbeak	38	39	100	9	2.6	6 (2)
Indigo Bunting	119	24	99	20	4.5	6 (3)
Orchard Oriole	96	16	99	20	4.0	7 (4)

[a] Number of observations.
[b] Percent of flock subtotal in single-species groups.
[c] Number of single-species groups observed.
[c] Percent of single-specics groups consisting of only two individuals. Number of male-female pairs noted parenthetically.

viduals of at least 18 species were discovered in the surf or on the beach during daily walks along a 2-km stretch of beach. This "sample" is a conservative indication of mortality because carcasses are consumed or buried by crabs or other scavengers. The most frequently found species (*Catharus* thrushes, Scarlet Tanagers) winter in South America and often arrive on the barrier islands in a fat-depleted condition (Kuenzi 1989).

Thirteen individuals of five species were found dead in the interior of the island, presumably of starvation: Purple Martin (*Progne subis*) (N = 7, mean mass = 34.6 g), Indigo Bunting (N = 3, mean mass = 9.5 g), Tree Swallow (*Iridoprocne bicolor*) (N = 1, mass = 12.2 g), Red-eyed Vireo (N = 1), and Hooded Warbler (N = 1, mass = 7.7 g). These masses are near fat-free values (Kuenzi 1989) and carcasses were devoid of visible subcutaneous fat (see Helms and Drury 1960). The remains of 12 individuals of at least five species were found on the island during the study period and had evidently been preyed upon by raptors. Although few

TABLE 5

RAPTORS OBSERVED ON HORN ISLAND BETWEEN 21 MARCH AND 10 MAY 1987

Species	N[a]	No. individuals	Habitat	Dates (early/late)
Swallow-tailed Kite[b] *Elanoides forficatus*	5	4	Forest: in flight and hunting	24 Mar/30 Apr
Northern Harrier *Circus cyaneus*	3	3	Marsh/meadow: in flight and hunting	26 Mar/2 Apr
Sharp-shinned Hawk[c] *Accipiter striatus*	13	12	Forest: in flight	26 Mar/26 Apr
Cooper's Hawk *A. cooperi*	1	1	Forest: in flight	24 Mar
Red-tailed Hawk *Buteo jamaicensis*	2	1	Marsh/meadow: in flight and perched	5 Apr/7 Apr
American Kestrel[d] *Falco sparverius*	14	8	Marsh/meadow and edge: in flight, hunting and perched	29 Mar/25 Apr
Merlin[d] *F. columbarius*	24	20	Marsh/meadow, edge and forest clearings: in flight, hunting and perched	22 Mar/9 May
Peregrine Falcon[d] *F. peregrinus*	15	12	Marsh/meadow and Dune: in flight, hunting and perched	21 Mar/8 May

[a] Number of sightings.
[b] Observed foraging extensively on insects (aerial capture).
[c] Observed chasing passerines (captures not observed, though evidence of successful prey capture was found).
[d] Observed chasing, capturing, and feeding on passerines.

instances of predation were observed, sightings of raptors on the island were numerous during migration and were associated most often with the Marsh/Meadow and Forest (pine) habitat types (Table 5). In the former habitat, those predators perched on isolated trees from where they watched for prey. Several Merlins and Peregrine Falcons spent consecutive days on the island, frequenting the same perches. Five of eight raptor species and 87% of 61 individual raptors observed during the study prey on small birds.

DISCUSSION

Counts of birds on Horn Island during the spring of 1987 indicate that most trans-Gulf migration occurred from mid-April through early May, which coincides with seasonally favorable weather for crossing the Gulf of Mexico (Buskirk 1980). The seasonal pattern of trans-Gulf migration revealed in our study corroborates the pattern found by mist-netting migrants on an adjacent barrier island (Kuenzi 1989) and in coastal Lou-

isiana (Moore, unpubl. data) as well as radar observations made by Gauthreaux (1968) in coastal Louisiana.

Males of several species appeared on Horn Island before females in the spring of 1987. Francis and Cooke (1986) found that the difference between sexes among several paruline warblers at Prince Edward Point, Ontario, ranged from two to six days and differed most in species that arrived earliest. Although data more comparable to the Ontario study are needed from the northern Gulf coast before differential passage can be compared latitudinally, our results suggest that males depart earlier from neotropical wintering grounds rather than migrating at a faster rate than females (i.e., make fewer stopovers and/or stopover for a shorter time). If the latter were the case, the difference in time-of-arrival at stopover sites should increase as migrants approach breeding areas and should be minimal following trans-Gulf migration.

Our sample sizes probably reflect a surplus of males on the island. Because females cross the Gulf of Mexico later than males and because the probability of favorable weather for ongoing migration increases as the season progresses (Buskirk 1980), fewer females stopover on the island. Although females may be less conspicuous than males during stopover, the sexes do not appear to differ in the habitats they used on the island nor do sexes differ in microhabitat use (within habitats) during stopover (Moore pers. obs.).

Habitat use.—Habitat use during migration has profound consequences for a bird's: (1) ability to satisfy energy requirements, (2) vulnerability to predators, and (3) exposure to environmental stress. Migrants cannot search for the best stopover habitat (sensu Hutto 1985) and may be forced to use sub-optimal sites, especially after crossing an ecological barrier. Besides the availability of suitable habitat (Fretwell and Lucas 1970), habitat selection during migration depends on the time available to search for superior habitats (Ward 1987). For a fat-depleted migrant, the benefits of rejecting suboptimal habitats may be outweighed by the cost of failing to find the "best" habitat. Extrinsic (extra-habitat) factors, such as accessibility of stopover habitats, could override ranking of habitats based on within-habitat criteria such as food availability (Hutto 1985). For example, the peak of trans-Gulf migration occurs in the latter half of April and early May, and it corresponds to a period of strong southerly airflow with infrequent frontal activity (Buskirk 1980). Unfavorable weather associated with frontal activity (i.e., northerly winds and precipitation) occasionally extends south to the Gulf coast and into the Gulf of Mexico and forces migrants to "fallout" when and where they might not otherwise

stopover (Lowery 1955; Gauthreaux 1971, 1972; Moore and Kerlinger 1987).

Nevertheless, when trans-Gulf migrants stopover on Horn Island, they select certain habitats. In most cases, we can only speculate as to why certain habitats were attractive to migrants. The selection of open habitats by Eastern Kingbirds, for example, was probably related to the bird's propensity to hawk prey items (pers. obs.). Presumably Scrub/Shrub was attractive because it offered refuge from predators as well as adequate food. Moreover, we cannot conclude how specific are the implied preferences. Patterns of use extended across three widely used habitat types, though five of the 20 species included in Table 2 clearly preferred Scrub/Shrub. Because long-distance migrants make repeated and temporary use of stopover habitats that normally differ in vegetation structure, resource quality and quantity, and competitive pressures, flexibility in the use of habitat would be expected during migration. This flexibility provides the basis for immediate responses to the energy demands of migration (Morse 1971, Loria 1988).

Although habitat selection in areas of stopover may be innate (Bairlein 1983), identification of suitable habitat undoubtedly requires time for migrants to familiarize themselves with the distribution and availability of resources. Two observations suggest that migrants settle in a habitat according to some ranking based on exploration (see Hutto 1985): (1) When migrants first arrive they "stream" through habitats in loose mixed-species groups and seldom feed. Shortly thereafter, they are usually found foraging alone or in small single-species flocks. (2) The difference in habitat use we found between morning and afternoon samples suggests that migrants adjusted their use of habitat types following exploration. Because most trans-Gulf migrants arrived over the northern Gulf coast after 10:00 h (see Gauthreaux 1971, 1972) and because many of the birds that stopped during the day left the island the evening of their arrival (Moore and Kerlinger 1987, Kuenzi 1989), migrants observed during afternoon (pm) censuses are likely to be birds that arrived that day, whereas birds observed during morning (am) censuses are birds that spent at least one day on the island. Changes in habitat use over the course of a day might also reflect diel changes in prey availability (e.g., Hutto 1981) or energetic constraints. Lean birds might broaden their use of habitats in response to heightened energy demand much as they do microhabitat utilization (see Loria 1988).

Flocking.—Most passerines that cross the Gulf of Mexico initiate migration at night and reach the northern Gulf coast during daylight (Lowery 1955, Gauthreaux 1971). The diel timing of arrival on the northern Gulf

coast depends on wind and weather conditions over the Gulf of Mexico, with peak densities between 10:00 and 14:00 CST (Gauthreaux 1971). The majority of birds fly in compact flocks at an altitude of 1200 to 1500 m (Gauthreaux 1971) at that time and remain in flocks at stopover sites (Gauthreaux 1972, Rappole and Warner 1976).

Flocking could improve a migrant's chance of finding suitable habitat and adequate food. Once suitable habitat was located on Horn Island, many migrants foraged alone, while others continued to forage in small flocks. Our observations on the presence and behavior of bird-eating raptors on Horn Island suggests that predation is a significant risk to migrants and group foraging could decrease the probability of predation (Morse 1977, Pulliam and Millikan 1982; but see Lindstrom 1989). Less time spent scanning for predators and more time searching for food would be especially important for a fat-depleted migrant following trans-Gulf migration.

Flocks on Horn Island were usually small and homogeneous in composition. Although social foraging may enhance rates of food intake for migrants, the small flock sizes observed in our study may reflect a decrease in flocking tendency because food requirements are high relative to expected food intake (Pulliam and Millikan 1982). When fat-depleted migrants arrive on Horn Island, they are unfamiliar with the distribution and abundance of food, and expected food intake is unknown.

We often observed groups of two or three birds, including both sexes, which is consistent with speculation that some individuals form pairbonds prior to arrival on the breeding site (Greenberg and Gradwohl 1981). However, migrants are believed to fly singly or in loose groups at night (Balcomb 1977), which would make it difficult for pairs to remain together. Recent observations of "marked" Prothonotary Warblers suggest that trans-Gulf migrants may depart from the same location, maintain contact while flying at night, and form flocks the next morning over the northern Gulf Coast (Moore 1990).

Mortality.—Pienkowski and Evans (1985) observed that "[T]he remarkable lengths of regular migratory journeys by many birds are now so well established that some biologists seem to discount their costs." Mortality during migration, though difficult to estimate, may be substantial (Lack 1946, Moreau 1972, Ketterson and Nolan 1982). Our observations reveal that migratory birds are preyed upon during stopovers, suffer starvation when they stopover in an energetically stressed condition, and succumb to adverse weather during migration.

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BREEDING ECOLOGY OF SEASIDE SPARROWS IN A MASSACHUSETTS SALT MARSH

ROBERT M. MARSHALL AND STEVEN E. REINERT[1]

ABSTRACT.—Seaside Sparrows (*Ammodramus maritimus*) were observed during the breeding seasons of 1985 and 1986 in a 151-ha salt marsh/tidal pond complex in Massachusetts near the northern range limit for the species. The study marsh is ditched and is dominated by salt meadow grasses (*Spartina patens, Distichlis spicata, Juncus gerardi*) and the high marsh form of *Spartina alterniflora*. Territories generally were isolated from one another; however, six relatively small territories were clustered into an area of the marsh rich in suitable nesting and foraging sites. The mean size of 17 territories measured in 1985 was 3953 m². Territories contained more tidal creek, medium-height *S. alterniflora*, and persistent-growth *S. alterniflora* than was expected, based on the results of line-intercept vegetation sampling done within randomly placed plots. Eighty-two percent of 60 nests found were placed in irregularly flooded *S. alterniflora* habitats, and 54% were placed in medium height *S. alterniflora* stands that occurred as approximately 2-m wide strips adjacent to creeks and ditches. One-half of all nests found were lost to flooding by spring tides which simultaneously destroyed most active nests on the marsh in May of each year. The rapid renesting response of most sparrow pairs following flooding events resulted in a synchronization of nesting activities with the tidal cycle. Synchronized nests had an enhanced probability of survival since the nesting cycle could be completed prior to the next spring tidal inundation. Overall, nest success was highest for nests initiated after 20 June, due to the increased probability of renesting attempts being synchronized to the tidal cycle, and because of the seasonal growth of marsh grasses which provided a more elevated nest substrate. *Received 6 June 1989, accepted 1 Nov. 1989.*

Although substantial work has been done on populations of the northern race of the Seaside Sparrow (*Ammodramus m. maritimus*) occupying Long Island, New York, marshes (Post 1974; Post and Greenlaw 1975, 1982; Greenlaw 1983; Post et al. 1983; Greenlaw and Post 1985), few investigations have been conducted in southern New England, close to the northern range limit for the species. Here populations are uncommon and relatively small, and are susceptible to local extirpation. Reinert et al. (1981), Stoll and Golet (1983), and DeRagon (1988) have conducted the only recent New England studies. They determined patterns of Seaside Sparrow habitat use in Rhode Island salt marshes.

In this paper, we report on aspects of habitat selection and breeding biology of a Massachusetts Seaside Sparrow population (ca 24 pairs) occurring only 137 km south of the northern range limit of the species. Our

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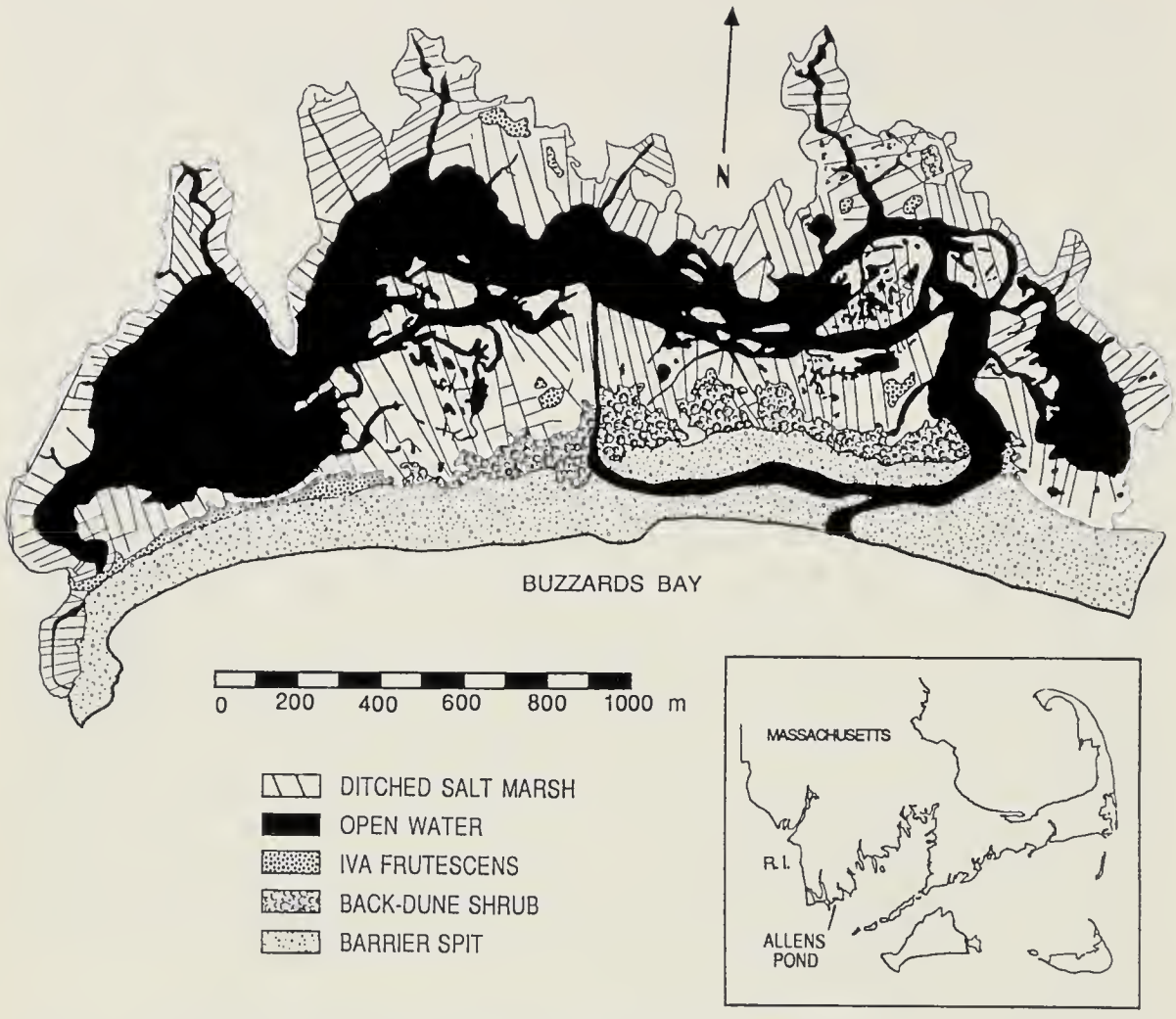

FIG. 1. Allen's Pond, South Dartmouth, Massachusetts, illustrating the intensity of mosquito ditching in the salt marsh. Back-dune shrub is dominated by bayberry (*Myrica pensylvanica*) and poison ivy (*Rhus radicans*).

study site differs substantially from other North Atlantic marshes inhabited by this race in the distribution and composition of marsh vegetation, frequency of catastrophic flooding events, and resultant patterns of habitat selection and mortality. We address such differences as they relate to patterns of Seaside Sparrow habitat use and factors affecting nest success.

STUDY AREA

Allen's Pond is a 67-ha tidal pond located in South Dartmouth, Bristol County, Massachusetts (41°31′N; 71°00′W). The pond is connected to Buzzards Bay by a tidal inlet (Fig. 1), and is bordered on all sides by salt marsh totaling 91 ha. A 35-ha barrier beach/dune system lies adjacent to the salt marsh to the south, with maritime oak forest, agricultural fields, and shrub communities bordering to the east, north, and west.

Prior to mid-century, the salt marsh was ditched extensively for mosquito control (Fig. 1). Linear ditches, 0.5–1.0 m wide, transect the salt marsh at 30 to 40-m intervals throughout its entire expanse, extending from Allen's Pond to the upland edge of the marsh. Although

most ditches remain open, they have not been maintained and many have become filled to varying degrees, lessening the flow of tidal water through them. To a lesser extent, naturally formed tidal creeks, and irregularly flooded pools occur throughout the marsh.

The interior of the marsh is dominated by irregularly flooded high marsh vegetation, chiefly *Spartina patens, Distichlis spicata,* and *Juncus gerardi* (hereafter "salt meadow"), and the short form (<40 cm) of *S. alterniflora* (hereafter "short SA"; Niering and Warren 1980, Greenlaw 1983). Sparse stands of short SA grow on the most poorly drained areas of the high marsh adjacent to, or mixed with, salt meadow graminoids. Although the tall (>100 cm) low marsh (regularly flooded) form of *S. alterniflora* is nearly absent, an irregularly flooded, intermediate form (40–100 cm tall) (hereafter "medium SA"; Greenlaw 1983), grows in a zone between the elevations of the low marsh and salt meadow. Medium SA most commonly grows in dense 1- to 2-m wide stands along creeks, ponds, and mosquito ditches (hereafter "water-side SA"). It often persists as clumped, erect, brown stems throughout the winter and subsequent growing season. Stands of medium SA sometimes extend 10–20 m into the marsh interior and, in some areas fill the entire inter-ditch span. Where short SA grows adjacent to water, it also forms dense, persistent stands, similar to medium SA in all aspects but height.

Small islands (4–100 m^2) created by the deposition of spoil are scattered throughout the marsh and are dominated by *Iva frutescens* and *J. gerardi.* Those plants are also dominant where the tidal marsh grades into the upland.

METHODS

Observations of Seaside Sparrows were made between 05:00 and 10:00 or 18:00 and 20:30 EST on 46 days from 1 May–25 August in 1985, and on 61 days from 30 April–22 August in 1986. Adults were trapped with mist nets and banded with a U.S. Fish and Wildlife Service aluminum band on one leg and a unique combination of two colored celluloid bands on the opposite leg. Nestlings were banded five to six days after hatching with an aluminum band placed on the right leg in 1985 and on the left in 1986. We banded 13 adult (seven male, six female) and 35 nestling Seaside Sparrows in 1985, and 18 adults (12 male, six female) and 58 nestlings in 1986. Territories were mapped using the flush method (Wiens 1969) and by observing birds remotely with the aid of a spotting scope. Songposts were plotted on 1:985 scale cover maps of the area. Territories were delineated by connecting the outermost songpost plots on the cover maps (Odum and Kuenzler 1955), and territory size was subsequently determined with a compensating polar planimeter.

In 1985, the percent cover of each habitat occurring within 17 Seaside Sparrow territories and 17 randomly located circular plots was estimated by the line-intercept method (Canfield 1941, Reinert and Golet 1979). Each random plot was 3953 m^2, the mean area of the 17 Seaside Sparrow territories. Sampling was done along two perpendicular transect lines which crossed at the center of the territory/plot. The habitat composition was not estimated within seven territories for which we had inadequate data on territory boundaries. We tested for significant differences ($P \leq 0.05$) in habitat composition between territories and random plots, using unpaired t-tests for each habitat type. Plant height measurements were made within all *S. alterniflora* segments. Measurements were made at the center of segments <5 m in length, and at four evenly spaced points within segments >5 m. In addition, the presence or absence of persistent stems was noted for each *S. alterniflora* patch intercepted.

For each nest located, the height of the nest (substrate to rim), height of surrounding vegetation, and distance to nearest open water were measured. Nests were visited approximately every four days during nest building and egg-laying and every other day during the incubation and nestling stages. We used the methods of Mayfield (1975) and Ricklefs and Bloom (1977), respectively, to calculate nest success and breeding productivity.

RESULTS

Population size and philopatry.—Twenty-four mated males occupied the study area during the 1985 breeding season. In 1986, 29 males were located, 24 of which were mated. In each year, males arrived during the first week of May, and females were first observed during the third week of May. Four (30.8%) of 13 adult Seaside Sparrows banded on the study area in 1985 returned in 1986. The territories of three (two male, one female) overlapped those which they occupied in 1985, and the territory of the fourth bird (male) was approximately 100 m from that defended in 1985. None of the 35 nestlings banded in 1985 was seen in the study area in 1986.

Territories.—The mean size of 17 territories for which adequate boundaries were determined in 1985 was 3953 m^2 (range = 1290–10,423 m^2). During both years, a central portion of the marsh, where tidal creeks, pools, and mosquito ditches are relatively abundant, contained an aggregation of six territories whose boundaries were adjacent or overlapping. The remaining territories were widely distributed throughout the marsh in each year. The aggregated territories were significantly smaller (t = 2.23; $P < 0.05$) than isolated territories ($\bar{x}$ = 1814 m^2 vs 4730 m^2, range = 1290–2581 m^2 vs 1411–10,423 m^2, N = 6 vs 11, respectively).

Male Seaside Sparrows which occupied territories within the interior of the marsh perched and sang nearly exclusively from patches of clumped, persistent vegetation, especially from stands of water-side SA. Stems of *I. frutescens* and *Phragmites australis* were the most frequently used song-posts of males which occupied territories near the upland edge of the marsh.

Our observations indicate that Seaside Sparrows foraged exclusively within territory boundaries, and although we did not quantify the use of habitats for foraging, our observations revealed that the banks and exposed bottoms of mosquito ditches and tidal creeks were the principal foraging areas. Birds also foraged within sparse stands of short SA when it was available within their territories.

Fig. 2 compares the habitat composition of Seaside Sparrow territories with that of the random plots. There was a significant difference for tidal creek only, which was more abundant in territories ($\bar{x}$ percent cover = 18.0 vs 2.5, t = 3.6, $P < 0.001$). The six aggregated territories measured in 1985 contained more overall SA area (60 vs 40%), and water-side SA area (28 vs 17%), and less salt meadow (22 vs 38%), than the non-grouped territories. However, none of those differences was significant.

Nest-site selection.—Seaside Sparrow nest sites at Allen's Pond were categorized into three early-season (nests started on or before 20 June)

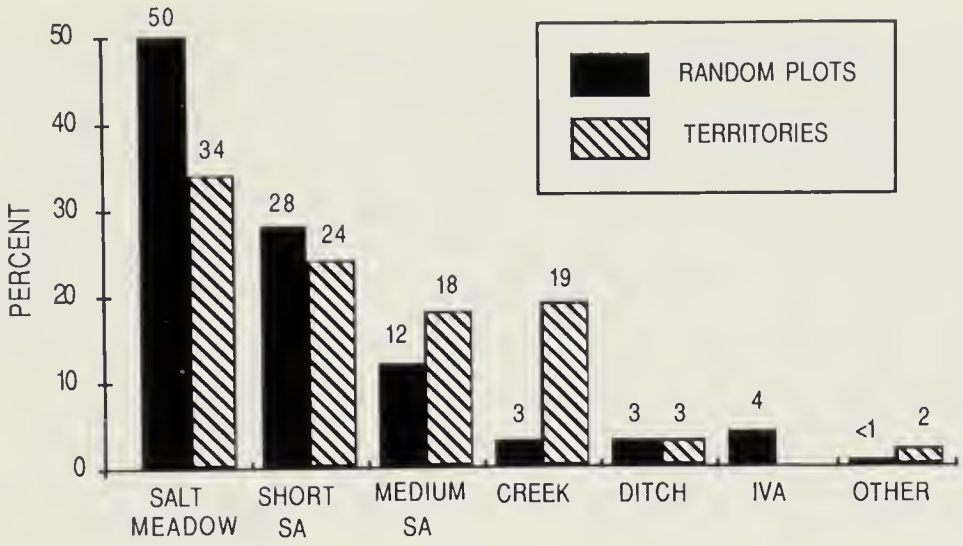

FIG. 2. Mean percent cover of habitats in 17 Seaside Sparrow territories and 17 random plots measured in 1985.

and two late-season (nests started after 20 June) types (Table 1). In both years, the height of new herbaceous vegetation exceeded that of persistent stems on or before 20 June, after which new growth became the primary substrate within which nests were placed.

Eighty-seven percent of all early-season nests were placed in clumped and erect persistent vegetation. Medium height persistent *S. alterniflora* was the tallest herbaceous cover on the marsh at this time (Table 1), and

TABLE 1

NEST-SITE CHARACTERISTICS AND NEST SUCCESS OF EARLY- AND LATE-SEASON[a] SEASIDE SPARROW NESTS IN DIFFERENT HABITATS[b] IN 1985 AND 1986

	N	Mean (±SD) height of nest (cm)	Mean (±SE) height of vegetation at nest (cm)	Number of nests within 2 m of water (%)	Number of successful nests (%)[c]
Early-season nests					
Persistent SA	30	18.7 ± 4.54	42.1 ± 8.39	13 (43)	7 (23)
Persistent SM	4	15.5 ± 2.88	31.5 ± 5.44	0	1 (25)
New growth SM	5	11.4 ± 1.97	32.9 ± 8.74	3 (60)	1 (20)
Late-season nests					
New growth SA	19	21.9 ± 5.56	52.7 ± 14.82	14 (74)	13 (68)
New growth SM	2	12.0	38.8	1 (50)	1 (50)

[a] Early-season nests were initiated on or before 20 June; late-season nests were initiated after that date.
[b] SA = *Spartina alterniflora*, SM = salt meadow.
[c] Successful nest = at least one young fledged.

30 (77%) of 39 early-season nests were placed in this habitat. Three early-season nests (8%) were placed in stands of persistent *D. spicata,* and one nest was placed in a mix of *S. patens* and *S. alterniflora.* Four of the remaining five (10% of total) early nests were placed within new growth *J. gerardi* which attained its maximum height by mid-June. One nest was placed in a stand of new growth *S. patens* on an elevated spoil bank.

Nineteen (90%) of 21 late-season nests were placed in new growth *S. alterniflora* habitats. The *S. alterniflora* stems surrounding those nests were significantly taller than the persistent stems that surrounded early-season *S. alterniflora* nests ($\bar{x}$ = 52.7 vs 42.1 cm, respectively; t = 2.83, $P < 0.001$), and late season *S. alterniflora* nests were significantly higher than early-season nests ($\bar{x}$ = 21.9 vs 18.7 cm, respectively; t = 2.13, $P < 0.04$) (Table 1). The two remaining late-season nests were placed in new growth *J. gerardi.*

Thirty-one (54%) nests were placed in stands of water-side SA. Those stands were significantly taller than stands of *S. alterniflora* occurring more than 2 m from water bodies ($\bar{x}$ = 51 vs 31 cm, t = 10.45, $P < 0.001$), and the nests placed within them were significantly higher than other *S. alterniflora* nests ($\bar{x}$ = 20.3 vs 16.8 cm, t = 2.70, $P < 0.009$). Also, stems of persistent *S. alterniflora* occurred more frequently in water-side stands than in other stands of *S. alterniflora* (50 vs 20%). Twenty (65%) of the water-side nests were placed adjacent to mosquito ditches and 11 (35%) adjacent to tidal creeks.

Nesting biology.—The first known egg dates for 1985 and 1986 were 25 May and 26 May, respectively. The last known egg-laying date in 1985 was 7 July, and in 1986 was 30 July. The mean clutch size was 4.0 (N = 30) in 1985 and 3.9 (N = 25) in 1986. Clutch size in 1985 ranged from three (four nests) to five eggs (two nests) and in 1986 from two (one nest) to five eggs (one nest). The single two-egg clutch (1986) was initiated by a pair that was still tending to a single young which had left the previous nest only six days earlier. All five-egg clutches were laid during first nest attempts.

Observations of nine nests found during egg laying indicate that incubation began with the laying of the last egg. The mean incubation period (number of days from last egg laid to last egg hatched) for seven nests with complete data was 12.4 ± 0.97 days (range = 11–14 days).

The mean nestling period (number days from first egg hatched to first young fledged) during both years was 9.6 ± 0.51 days (N = 22; range = 9–11 days).

We observed the total number of days elapsed from the initiation of nest construction to the fledging of the last young for 12 nests found

during both years. Two nestings were completed in 27 days, eight in 28 days, one in 30 days, and one in 36 days ($\bar{x}$ = 28.7 days).

Nest failure and renesting.—Due to the destruction of nests by spring and/or storm-driven tidal flooding, nesting attempts for many pairs were interrupted up to three times during both years. Of 60 nesting attempts observed during both years, 37 (62%) were unsuccessful. Of the nests lost, 81% were destroyed by spring tide flooding events (three events in 1985 and two in 1986), 5% were destroyed by a storm tide, and 3% were lost during two continuous days of rain and cold temperatures. Nest predation was not witnessed, but American Crows (*Corvus brachyrhynchos*) and Common Grackles (*Quiscalus quiscula*) were believed to be responsible for 11% of the nest losses.

Seaside Sparrows repeatedly renested following nest failure, and they also renested after fledging young from a previous nest. For both years combined, we documented that 16 pairs nested at least twice, and seven pairs nested at least three times. However, based on all evidence (e.g., empty nests found, behavior of adults), we suspected that 25 pairs nested at least twice and that 14 pairs nested three times.

We obtained complete chronological data for four renests following nest destruction. The mean inter-nest period (the number of days from nest failure to the day the first egg of the new clutch is laid) for those nests was 6.25 ± 1.7 days (range = 4–8 days). By back-dating from a known hatch date (assuming a 12-day incubation period and laying rate of one egg per day), we estimated a mean inter-nest period of 5.7 ± 1.0 days for an additional 11 nests initiated following nest failure (five days, N = 6; six days, N = 3; seven days, N = 1; eight days, N = 1).

In 1985 one female laid the third egg of a new clutch on the same day the single young from the previous nest fledged. We estimated inter-nest periods of eight and nine days from two nests in which at least one young fledged successfully from the previous nest attempt.

Nest success.—We defined a successful nest as that from which at least one nestling fledged. In 1985, 33 nest attempts produced 13 (39%) successful nests and 37 fledglings. In 1986, 27 nest attempts produced 10 (37%) successful nests and 27 fledglings.

Measures of the success rate (Mayfield 1975) for early- and late-season nests are presented in Table 2. In both years, most young fledged in July from second or third nest attempts of their parents (Fig. 3). Because most pairs renested immediately following nest loss, the simultaneous loss of many early-season nests due to tidal inundation acted to synchronize the subsequent nesting attempts of the unsuccessful pairs (Fig. 3). The young of those renesting pairs fledged nearly simultaneously, just prior to, or at

TABLE 2

NEST SUCCESS OF EARLY- AND LATE-SEASON[a] SEASIDE SPARROW NESTS

	1985			1986		
	Early-season nests	Late-season nests	Overall	Early-season nests	Late-season nests	Overall
Number of nests	20	10	30	14	11	25
Mean clutch size	4.1	3.8	4.0	3.8	4.0	3.9
Clutch survival[b]	0.347	1.0	0.482	0.888	1.0	0.945
Brood survival[b]	0.408	0.777	0.579	0.480	0.589	0.536
Probability egg will produce fledgling	0.108	0.637	0.221	0.326	0.548	0.426

[a] Early season nests were initiated on or before 20 June; late season nests were initiated after that date.
[b] After Mayfield (1975); based on 12 day incubation period, and/or 10 day nestling period.

the time of, the next spring tide (Fig. 3). Nest cycles extended as little as one day due to large clutches, or protracted incubation or nestling periods, were subject to destruction if their nests were not high enough to avoid the tides. We witnessed nestling sparrows literally climb from their nests as they avoided encroaching tides, and in one nest we observed a nestling drown two siblings while elevating its own body above the flood-water.

Late-season nests were also higher than early nests as a result of the seasonal growth of *S. alterniflora* which supported most of them (Table 2). For the two years combined, 68% of all young fledged from late-season nests that were placed in the taller new-growth *S. alterniflora.* Overall, 83% of all young fledged from *S. alterniflora* nests.

Successful early-season nest attempts of the two years resulted when either: (1) nest elevation was particularly high and flood waters were avoided, or (2) nests were flooded during the egg-laying period when eggs did not float from them.

Due to the high success rate of late-season nests in 1985, overall productivity (number of young fledged per female; Ricklefs and Bloom 1977) was greater in that year than in 1986 (4.47 vs 3.46 young/female, respectively). However, the probability of an egg producing a fledgling was greater in 1986 due to the greater proportion of eggs that survived to the nestling stage (Table 2). Ninety percent (87 of 97) of all eggs hatched in 1986, whereas only 56% (70 of 124) of all eggs hatched in 1985.

DISCUSSION

Nest success.—Factors relating to nest success in the Northern Seaside Sparrow have been documented for only two geographic areas: the south shore of Long Island, New York (Post 1974, Post and Greenlaw 1982,

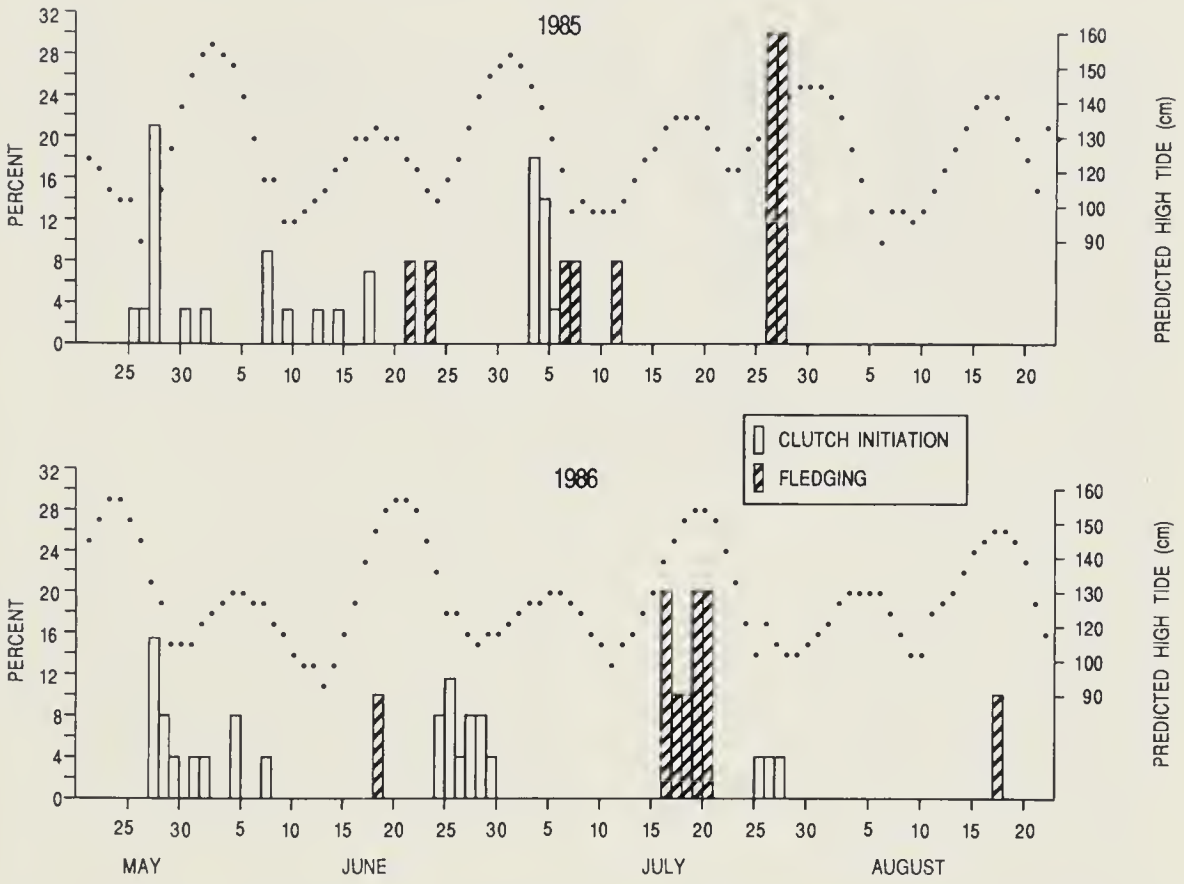

FIG. 3. Seasonal distribution of clutch initiation and fledging events in relation to the monthly tidal cycle. Bars represent the percent of total events, plots represent the predicted elevation of daily high tides relative to mean sea level for Newport, Rhode Island (White 1985, 1986).

Post et al. 1983), and our Allen's Pond study site in southeastern Massachusetts. In both areas, nest mortality was high, and nest failure related principally to catastrophic flooding events which destroyed, simultaneously, most active nests on the marsh. Predation rates were low at both sites. Flooding events in New York were associated with wind-driven tides and rain associated with storms; spring (moon) high tides under normal circumstances did not flood nests. At Allen's Pond, however, two spring tide flooding events in 1985 and 1986 reached sufficient elevation to destroy most nests. Thus, potentially catastrophic events occurred, predictably, every 28 days with the onset of spring tide cycles.

Because of this phenomenon, the renesting response of sparrows following nest loss, and the height of the nest, were the principal factors relating to nest success in this population. The probability of fledging young was greatest for late-season nests when marsh vegetation was tallest, and when nesting activities were more likely to be synchronized to the tidal cycle due to previous spring-tide related nest destruction.

TABLE 3

HABITAT AND TERRITORY CHARACTERISTICS OF SEASIDE SPARROW POPULATIONS IN THE NORTHEAST

	Ditched marches				Undithched marshes	
	New Jersey[a]	New York[b]	Rhode Island[c]	Massachusetts[d]	New York[b]	Rhode Island[c]
Mean size of territories (m^2)	—	4669	9010	4730[e] 1814[f]	484	4545
Territory type(s)	(1) Separate nesting and feeding (2) All purpose	All purpose[g]	All purpose[g]	All purpose[g]	Defended nesting with communal feeding area	(1) Separate nesting and feeding (2) All purpose
Distribution pattern(s) of territories	Widely spaced	Widely spaced	Widely spaced	(1) Widely spaced (2) Clustered	Clustered	Clustered
Dominant marsh vegetation	Salt meadow	Salt meadow	Salt meadow	Salt meadow	Medium SA	Medium SA
Nest site type(s) (n)	Juncus/Iva (8)	Salt meadow	(1) Juncus/Iva (1) (2) Medium SA (1)	(1) Medium SA (49) (2) Salt meadow (11)	Medium SA	(1) Medium SA (26) (2) Salt meadow (6)

[a] Woolfenden (1956).
[b] Post (1974).
[c] DeRagon (1988).
[d] This study.
[e] Mean size of 11, non-clustered territories (see Results).
[f] Mean size of 6 clustered territories (see Results).
[g] Type A territories of Nice (1937).

The length of breeding season, probability of an egg producing a fledgling, and overall productivity were similar between our Allen's Pond study site and the New York populations (Post and Greenlaw 1982). However, the total number of young recruited per unit area of marsh should be much greater in New York, since nearly all suitable habitat is occupied (Greenlaw 1983). Expansive areas containing apparently suitable habitat (as assessed by early-season availability of cover) were left unoccupied by Seaside Sparrows at Allen's Pond.

Habitat use.—For northern-race populations of the Seaside Sparrow, nest site requirements are commonly met in one of two types of marsh vegetation. In the first, nests are placed within erect clumps of persistent or new-growth medium SA (Post 1974, Greenlaw 1983, DeRagon 1988, the present study). Medium SA nest sites are most commonly used on poorly drained, unditched marshes where *S. alterniflora* habitats are abundant. Territories on these marshes typically are clustered and relatively small (Table 3). In the second type, nests are placed in the cover of the salt meadow graminoids, *S. patens, D. spicata,* or, most commonly, *J. gerardi,* which occur on relatively high areas of the marsh. These nest sites typically are used on salt-meadow dominant marshes that have been ditched for mosquito control. *S. alterniflora* habitats are not abundant, and patches of *J. gerardi/I. frutescens* prevail on spoil islands or spoil ridges which occur adjacent to the ditches (Woolfenden 1956, Post 1974, Greenlaw 1983, DeRagon 1988, the present study). Territories on these marshes are generally large and widely spaced (Table 3).

Among marshes where investigations of the northern race of the Seaside Sparrow have been conducted, Allen's Pond is unique in that each type of nesting habitat that has been documented for the species (see above) is widely distributed throughout the marsh. Foraging habitats, including ditches, creeks, and short SA, are also widely distributed. Although the marsh is dominated by salt meadow habitats, the widespread distribution of ditches and creeks (Fig. 1), each bordered by medium SA habitat, serves to break up the marsh physiognomy and create an interspersion of habitats which provides Seaside Sparrows a variety of habitat-use choices throughout the marsh. This configuration of habitats at Allen's Pond provided a natural experiment for determining nest-site preference. Although medium SA made up only 12% of the cover on the marsh, 82% of the nests were placed in that habitat. Only 18% of the nests were placed in salt meadow habitats which covered one-half of the marsh. This clearly indicates a preference for *S. alterniflora* nest sites, regardless of the fact that it was present in the form of narrow strips adjacent to ditches and creeks. Thus, although marshes ditched for mosquito control have been associated with salt-meadow nest sites in widely spaced territories and relatively

low population densities, it is clear that the composition and configuration of marsh habitats, regardless of prior ditching history, determines the manner in which Seaside Sparrows will utilize marsh resources.

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SHORT COMMUNICATIONS

Genetic variation in the Common Yellowthroat and some allies.—Considerable effort has been expended to document the nature of genetic variation at protein-coding loci within and among natural populations (Avise and Aquadro 1982, Lewontin 1985). Knowledge of intraspecific genetic variation can elucidate microevolutionary patterns and processes (Barrowclough 1983) and historical patterns of population fragmentation (Felsenstein 1982). Such genetic data also provide a perspective on the extent and organization of genetic variation among species. Relatively few studies of birds describe the geography of intraspecific genetic variation (Corbin 1983, Zink 1986, Zink et al. 1987, Johnson and Martin 1988) and genetic differentiation between species (Avise and Aquadro 1982). In this paper, we describe genetic variation within and among four populations of the Common Yellowthroat (*Geothlypis trichas*) and some congeners. Most of the taxa in the genus (with the exception of *G. poliocephala*) are essentially allopatric; hence, the species in the genus, excluding *G. poliocephala,* might constitute a group of allospecies. Our samples represent various geographic scales: "local scale"—populations of *G. trichas* representing three subspecies within Texas; "continental scale"—the samples from Texas plus Minnesota (*G. t. brachidactylus*) and Baja California (Mexico; *G. beldingi*); and "inter-continental scale"—congeners from Ecuador (*G. semiflava*) and Peru (*G. aequinoctialis*). The populations in south Texas inhabit areas that seem subject to periodic habitat extinctions (Klicka pers. obs.), which might lead to greater differentiation by founder events. Also, some or all of the south Texas samples and that of *G. beldingi* are from presumably resident populations, whereas the Minnesota population is migratory. Most studies of avian intraspecific genetic variation have included only migratory populations, and one might predict greater genetic differentiation among sedentary populations. Two taxa (*G. semiflava* and *G. aequinoctialis*) are considered full species, permitting comparison of within and between-species differentiation. In sum, our samples permit us to estimate the extent of genetic diversity at various levels within a genus distributed over two continents.

Methods.—We obtained tissue samples from 27 individuals in the Common Yellowthroat complex (Table 1); two specimens of *Oporornis* (MacGillivray's Warbler [*O. tolmei*] and Mourning Warbler [*O. philadelphicus*]) were used to estimate the genetic distance between the two genera. Within one hour of death, tissue samples from each specimen were placed on dry ice in the field, and upon return to the laboratory they were maintained at −70°C. Methods for preparation of tissue extracts and protein electrophoresis are documented elsewhere (Johnson et al. 1984, Zink 1986). Samples of tissue are retained in the Frozen Tissue Collection of the Museum of Natural Science, Louisiana State Univ. The computer program BIOSYS-1 (Swofford and Selander 1981) was used to compute allelic frequencies, Nei's (1978) and Rogers' (1972) genetic distances, and to construct a UPGMA phenogram and a distance-Wagner network. A computer program written by G. Barrowclough was used to compute F_{st}-values following Wright (1978); F_{st} is a measure of the amount of genetic variance partitioned among geographic samples.

Results.—Of the 30 loci surveyed, 12 were monomorphic and fixed for the same allele in all taxa: *SOD-1,2* (Enzyme Commission 1.15.1.1), *CK-2* (2.7.3.2), *αGPD* (1.1.1.8), *SDH* (1.1.1.14), *LDH-1,2* (1.1.1.27), *GPI* (5.3.1.9), *MDH-1,2* (1.1.1.37), *LAP* (3.4.11), and a general protein. The remaining 18 loci were variable, either within one of the samples (heterozygote) or between two or more taxa (Table 2). Heterozygosity (Table 1) averaged across taxa is 0.06 (excluding Mourning and MacGillivray's warblers). The percentage of loci that were polymorphic averaged 20.6%. Our samples are too small to test for departures from Hardy-Weinberg equilibrium expectations for genotypic proportions. Nei's (1978)

TABLE 1

TAXA EXAMINED, LOCALITY OF SPECIMENS, SAMPLE SIZE, AVERAGE DIRECT COUNT HETEROZYGOSITY (H), AND PERCENTAGE OF LOCI POLYMORPHIC[a]

Taxon	Locality	N	H	Percent of polymorphic loci
1. *Geothlypis trichas brachidactylus*	Minnesota: Scott Co.	5	0.10	33.3
2. *G. t. chryseola*	Texas: Val Verde Co.	5	0.05	16.7
3. *G. t. insperata*	Texas: Cameron Co.	5	0.10	26.7
4. *G. t. trichas*	Texas: Aransas Co.	6	0.06	20.0
5. *G. beldingi*	Mexico: Baja California Sur	3	0.03	6.7
6. *G. aequinoctialis auricularis*	Peru: Dpto. Lambaueque	2	0.10	20.0

[a] Values for the single individuals of *G. semiflava* (sample 7, from Ecuador: Prov. Pichincha), *Oporornis tolmei* (sample 8, Louisiana: Cameron Par.), and *O. philadelphia* (sample 9, Louisiana: Cameron Par.) are not reported.

genetic distance (not shown; available from authors or can be computed from the data in Table 2) averaged 0.006 among the three Texas samples, 0.009 for Texas plus Minnesota samples, 0.034 for the North American samples, and 0.070 ± 0.04 (SD) for the North and South American samples. Values of F_{st} followed a similar pattern: 0.04, 0.04, 0.14, and 0.21 for these levels of comparison, respectively. Adding *G. beldingi* to the comparisons substantially increased the level of genetic differentiation, as does adding the South American taxa. To examine the relationship between geographic and genetic distance among samples, we computed a rank-order correlation coefficient between the two sets of values, in essence an examination of the isolation-by-distance effect. The correlation coefficient of 0.66 ($P \leq 0.05$) indicates a significant positive relationship between geographic distance and genetic differentiation. We included samples of *G. semiflava* and *G. aequinoctialis* on the hypothesis that the entire complex constitutes a recently evolved group of allospecies; otherwise, considering genetic differentiation among sympatric congeners has no necessary significance in relation to geography. The average genetic distance from the two *Oporornis* species to the yellowthroats was 0.109.

The two branching diagrams (not shown, available from authors) based on Rogers' (1972) genetic distance revealed the following: the Texas samples cluster together and are most similar to the Minnesota sample, and the remaining taxa are rather distinct from the aforementioned group and each other; we lack confidence in the pattern of relationships among the species.

Discussion.—Levels of genetic variation (Table 1) within our population samples are consistent with those observed for other birds (Corbin 1983). Of interest are the values of F_{st}. For most bird species, F_{st} is less than 0.05 (Barrowclough 1983). This value was obtained from relatively few studies of migratory temperate passerine birds, many of which did not span the entire range of the species. Our value of 0.04 for North American *Geothlypis* (excluding *G. beldingi*) exceeds that found by Zink (1986) in a survey of the highly phenotypically differentiated Fox Sparrow (*Passerella iliaca*) over a similar geographic extent and is similar to that found by Johnson and Zink (1983) for the sapsucker superspecies *Sphyrapicus varius* (which also includes *S. ruber* and *S. nuchalis*). Hence, the partitioning by taxonomists of phenotypic variation in *G. trichas* into 12 subspecies (Lowery and Monroe

TABLE 2
ALLELIC FREQUENCIES FOR VARIABLE LOCI[a]

Locus (E.C. No.)	Sample 1	2	3	4	5	6	7	8	9
EST-D	A	A	A	A	A	A (0.75) B (0.25)	A	A	A
NP	A	A	A	A (0.92) B (0.08)	A	A (0.5) C (0.5)	A	A	A
LA1	A (0.8) B (0.2)	A	A	A	A	C (0.75) D (0.25)	A	A	A
LA2	A (0.7) B (0.1) C (0.2)	A (0.7) C (0.3)	A	A	A	A (0.75) D (0.25)	A	A	A
LGG	A (0.9) B (0.1)	A	A	A	A	A	A	A	A
EAP	A	A	A (0.9) B (0.1)	A	A	A	A	A	A
GSR	A (0.6) B (0.4)	A (0.9) B (0.1)	A (0.9) C (0.1)	A	A	A	A	A	A
MPI	A (0.5) B (0.5)	A	A (0.7) B (0.2) C (0.1)	A (0.42) B (0.58)	A	A	B	A	A (0.5) B (0.5)

TABLE 2
CONTINUED

Locus (E.C. No.)	Sample 1	2	3	4	5	6	7	8	9
ADA	A (0.8) B (0.2)	A	A (0.7) C (0.3)	A	A (0.17) D (0.83)	A (0.25) D (0.5) E (0.25)	A	A	A
CK2	A	A	A (0.9) B (0.1)	A (0.92) C (0.08)	A	A	A	A	A
CGOT	A (0.9) B (0.1)	A	A	A	A	A	A	A	A
MGOT	A	A	A	A	A	A (0.75) B (0.25)	A	A	A
PGM	A	A (0.5) B (0.5)	A (0.7) B (0.3)	A (0.67) B (0.33)	A	A	A	A	A
GPD	A	A	A (0.9) B (0.1)	A	A	A	A	A	A
ICD	A (0.9) B (0.1)	A	A	A	A	A	A	A	A
FUM	A	A	A	A	B	C	C	C	A
ACON	A (0.7) B (0.1) C (0.2)	A (0.9) C (0.1)	A	A (0.92) B (0.08)	A	A	A	C	C
PPRO	A (0.7) B (0.2) C (0.1)	A (0.7) C (0.3)	A (0.6) B (0.1) C (0.3)	A (0.6) B (0.1) C (0.3)	A (0.67) D (0.33)	C	E	A	F

[a] Numbers in parentheses are frequencies; samples are identified in Table 1; locus nomenclature follows Gerwin and Zink (1989).

1968) seems consistent with a relatively high degree of genetic differentiation, but study of other subspecies is necessary. Our genetic data are equivocal with respect to thc influence of bottlenecks in south Texas and the migratory status of populations. For example, the average genetic distance among the three Texas samples, 0.006, is very low and is 50% of the average between the Texas and Minnesota samples, 0.012. Thus, geographic distance among demes (even when one, e.g., Minnesota, is migratory) seems more important than bottlenecking in promoting genetic differentiation in yellowthroats. However, the F_{st} of 0.04 among the samples from Texas and Minnesota is relatively high, and comparison of other migratory populations the same distance apart as our resident Texas populations is needed to distinguish between geographic distance and migratory tendency as influences on genetic differentiation (the three Texas samples could be part of a larger lineage that went through a bottleneck). In general, our data indicate that genetic surveys of nonmigratory avian species are needed to further our understanding of avian genetic population structure.

The taxonomic status of *G. beldingi* is uncertain, and has been considered a subspecies of *G. trichas* (Mayr and Short 1970) rather than a distinct species. The F_{st} value for the group including *G. beldingi,* 0.14, is higher than found for most avian intraspecific comparisons, suggesting that the group is: (1) simply older than most species surveyed electrophoretically, (2) monophyletic but containing two species, or (3) paraphyletic. In terms of F_{st} and genetic distance (0.07 from samples of *G. trichas*), *G. beldingi* is differentiated at a level consistent with most avian species, although genetic distance cannot be the sole arbiter of species limits (Johnson and Zink 1983).

Our F_{st} estimate of 0.21 calculated over the species of *Geothlypis* surveyed indicates considerable differentiation. Because *G. aequinoctialis* and *G. semiflava* are considered specifically distinct from *G. trichas,* our computation of F_{st} reflects a category such as allospecies, rather than the typical intraspecific meaning of this value. Genetic differentiation in the genus seems, based on our limited comparisons, to be consistent with other well differentiated avian genera. Others (e.g., Capparella 1988, Gerwin and Zink 1989) have documented considerable genetic differentiation within neotropical avian lineages relative to temperate lineages. However, the genetic distance from *G. semiflava* and *G. aequinoctialis* to the other taxa averages 0.10, which is within the range of values detected among temperate congeners. Thus, our data are consistent with the possibility that the species in *Geothylpis* are relatively recently evolved.

Our data set is limited in number of loci and in the sampling of taxa (and individuals) present in the genus. Hence, we are cautious in interpreting our data in a phylogenetic sense. The two *Oporornis* species are differentiated from *Geothlypis* at an average genetic distance (Nei 1978) of 0.11, a value exceeding that reported by others (Barrowclough and Corbin 1978, Avise et al. 1980); however, the same loci and species were not surveyed in these studies. The value of 0.11 is somewhat low for avian intergeneric comparisons, and future workers should evaluate the possibility of combining *Oporornis* and *Geothlypis,* as they are in some checklists. The main conclusion we draw is that the North American samples of *G. trichas* excluding *G. beldingi* seem genetically cohesive, and they may be a sister taxon to *G. beldingi. Geothlypis beldingi* is genetically closer to North American samples (D = 0.07) than to *G. aequinoctialis* (D = 0.097) or *G. semiflava* (D = 0.122). However, further interpretation awaits phylogenetic resolution of all *Geothlypis,* which is currently under study (P. Escalante P. pers. comm.).

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Growth of Monk Parakeets.—Growth characteristics of nestlings vary considerably among bird species. These may result from the diverse selective pressures these species experience. For example, species with open nests are more prone to predation and may have evolved comparatively high growth rates in order to reduce the time in the nest (Lack 1968). Also intra-specific variations in growth parameters among years or in relation to hatching order indicate that the ability of growth processes to respond to different conditions may have adaptive value (Ricklefs 1968, 1976).

Parrots offer interesting material for analysis in this respect, due to their extreme altriciality, slow growth, and completely asynchronous hatching. Unfortunately, data for the group are scarce. Growth curves are known for only seven species, and for most the data come from captive birds (Caccamise and Alexandro 1976; Caccamise 1980; Saunders 1982, 1986; Bucher 1983; Stamps et al. 1985). Unique among the Psittaciformes, the Monk Parakeet (*Myiopsitta monachus*) is not a true cavity-nester since it builds large enclosed communal nests made of sticks where several pairs breed independently (Forshaw 1973; Martella 1985).

In this work, we present the parameters that describe the growth curve of nestlings of *Myiopsitta monachus catita* in a wild population and examine their variation among years and in relation to the hatching order within a brood.

Study area and methods.—The study was carried out in an area of 600 ha, situated near Jesús María, Córdoba, Argentina (31°05′S, 64°11′W).

From the pre-laying period to fledging time (November to March) in 1985–1986, 1986–1987 and 1987–1988, all the parakeet nests situated below 7 m height were checked. In order to minimize disturbance caused by the observers, visits were spaced nine days on average (range 7–12).

The eggs were measured to the nearest 0.1 mm (length and breadth), weighed to the nearest 0.1 g, and individually marked with indelible ink. After hatching, the nestlings were initially identified by toenail clipping. Later they were banded with numbered aluminum bands. On each visit, the nestlings were weighed to the nearest 0.1 and 1 g, for the weights under and over 10 g, respectively.

All the nestlings found dead in the nest, as well as those that disappeared before the minimum fledging age (estimated as 35 days), were excluded in our calculations. Seven successful nestlings that showed signs of malnutrition or weight recession at an early age were not included. Also, and due to the fact that in this species there is a recession of weight at fledging, we truncated the data of each successful nestling at the maximum mass value observed up to 36 days after the first visit.

Logistic curves were fitted by following the trial-and-error least-squares method proposed by Brown (1979), which is based on testing the goodness of fit of a series of logistic growth curves generated by varying stepwise the parameters A, K, and W_0 (see definitions below) in all combinations over a reasonable range for each one of them. This method adapts better

to our data than that used by Ricklefs (1967), since the precise age of each nestling was known only in a few cases, and there were not enough points per chick to fit individual curves properly. However, by means of Ricklefs' method we obtained a rough estimate of each parameter in order to determine the intervals in which to iterate. The ranges used here to generate the trial curves included the 99.9% confidence interval for the mean of each parameter, previously calculated by Ricklefs' method in eleven birds from eleven broods whose ages were exactly known because they were found during hatching. Their initial weight was roughly determined by subtracting from the weight of the pipped egg the weight of the shell (estimated as 0.7 g). This probably slightly overestimates hatchling mass (because there is an additional loss of water at hatching), but as stated below, the accuracy of this parameter does not influence the results of the curve fitting process.

The age corresponding to the first observed mass for each nestling was estimated by solving the logistic equation: $W_d = A/(1 + e^{(-K(d-T))})$, in which W_d = mass (g) at d days of age, d = age of nestling in days, A = asymptotic mass (g), at which growth levels off just before fledging, K = growth rate constant (per day), e = base of natural logarithms, and T = $\ln(A/W_0 - 1)/K$, time, or age (specified in days) at inflection point of the curve, one half of the asymptotic weight.

The number of days between weighings was added to this value to obtain the estimated age at each visit. These ages were used in the logistic equation to calculate the respective predicted masses. The sum of squared deviations between observed and predicted masses of all nestlings was calculated for each trial curve.

To obtain the confidence intervals of the growth parameters we employed the Jackknife method, according to the criterion proposed by Bradley et al. (1984) and Brisbin et al. (1987). Ninety-five percent confidence intervals were calculated as suggested by Bradley et al. (1984): $I.C. = P \pm Et_{0=05.N-1)}$, where P = parameter estimator of the curve calculated by means of the least-squares method; E = standard error of the pseudo values; t = critical value of the t distribution; and N = number of independent pseudo values (cases).

Pseudo values were computed for three parameters of the growth curve (A, K, T). The complete set of data for each individual was considered as a simple case when taking the sub-samples. Thus, the pseudo values were obtained for each case rather than each separate point. In this way, we made sure that the calculated pseudo values were independent and overstating the degrees of freedom was avoided (Bradley et al. 1984). We consider that this method is reasonably accurate bearing in mind the large sample size employed (447 data points, representing a total of 128 nestlings with three to five weights available for each of them).

Results and comments.—Table 1 shows the set of parameters that give the lowest sum of squares by Brown's method when the pooled data of all the nestlings that fledged successfully in all years were analyzed. As Brown (1979) points out, the variation of the hatchling mass W_0 within its range (4.07–5.45 g) produced a negligible effect on the total sum of squares. Thus, the average W_0 calculated for the 11 nestlings of known age was taken as a constant during the iterations in order to reduce substantially the computing time.

The differences in asymptotic weight (A) between years are less than 1.1%, while in the growth constant (K) there is a maximum difference of 11.6%. The growth rates corresponding to the first two years were significantly higher ($P < 0.05$) when compared to that of the last by using the method proposed by Gabriel (1978). The relative constancy of A compared with the variations detected in K suggests that growth rate change responds to environmental conditions, extending the time needed to achieve the asymptotic mass.

The derived curve can be compared with the mass data points which were aged by using the curve, as well as with the masses of eleven birds of known age (Fig. 1). The fit of the curve to the data appears visually adequate in both cases. Notice that in many cases the

TABLE 1
PARAMETERS OF THE LOGISTIC GROWTH CURVE CALCULATED BY A LEAST SQUARES TRIAL-AND-ERROR METHOD[a]

Parameter	1985/1986	1986/1987	1987/1988	Pool	95% C.I.[b]
Asymptote (A), in g	103.2	103.9	104.3	103.9	102.5–105.3
Growth rate (K), per day	0.2598	0.2478	0.2327	0.2437	0.2498–0.2376
Inflection point (T), in days	11.40	11.98	13.07	12.46	12.11–12.81
Initial weight (W_0), in g	4.76	4.76	4.76	4.76	
T_{10-90}, in days	16.9	17.7	18.9	18.0	
No. nestlings	16	61	51	128	
No. broods	7	15	17	39	

[a] Increments during the iterations were 0.1 in A and 0.0001 in K.
[b] Obtained using jackknife method.

last weights were registered fairly after the fledging age because fledglings were taken by surprise inside the nest.

When the approximate time of fledging (35 to 40 days) is measured by using an index expressed in growth units (as defined by Ricklefs 1967), this age is equivalent to 2.50–3.06 growth units. These growth index values fall within the range of 2.5–3.5 growth units given by Ricklefs (1973) for most altricial land-birds.

Average adult weight at the end of the reproductive season (March) is 92.9 g (Navarro and Bucher unpubl. data). Thus, the ratio (R) between the asymptotic weight of nestlings and adult weight is 1.12. This value (over 1.10) does not correspond to a species such as the Monk Parakeet which has arboreal and ground feeding habits, but to a species which spend a large proportion of its foraging time in flight (Ricklefs 1968). However, this high R value coincides with what would be expected considering its long nestling period (Ricklefs 1976).

Nestling weight decreases by the time of fledging (Fig. 1), so the asymptote does not show the real mass at that moment. Based on the last weight registered for each successful nestling, we can estimate an average mass at fledging in 97.1 ± 8.38 g (SD) (N = 135).

The growth constant (K) obtained here is considerably below (25%) than the estimated by the allometric relationship for temperate altricial land-birds with an equivalent asymptote (Ricklefs 1968). However, it is 10% higher than the predicted value for tropical land-birds (Ricklefs 1976).

Our K value is higher than that for the cavity-nesting Psittaciformes studied by Bucher (1983). Given that K is inversely correlated with body size (Ricklefs 1968) and considering that three of those species have lower asymptotes than the Monk Parakeet, it is reasonable to attribute the discrepancies in K to the particular nesting habit exhibited by this parrot, bearing in mind that natural selection could favor a shorter nestling period in less protected nests (Lack 1968). The nest built by the Monk Parakeet, although safer than an open nest, is less secure than tree or cliff cavities. Falling of the nests due to strong winds is relatively frequent (pers. obs.), and important losses from vertebrate predators are common (Martella and Bucher 1984, Martella et al. 1985).

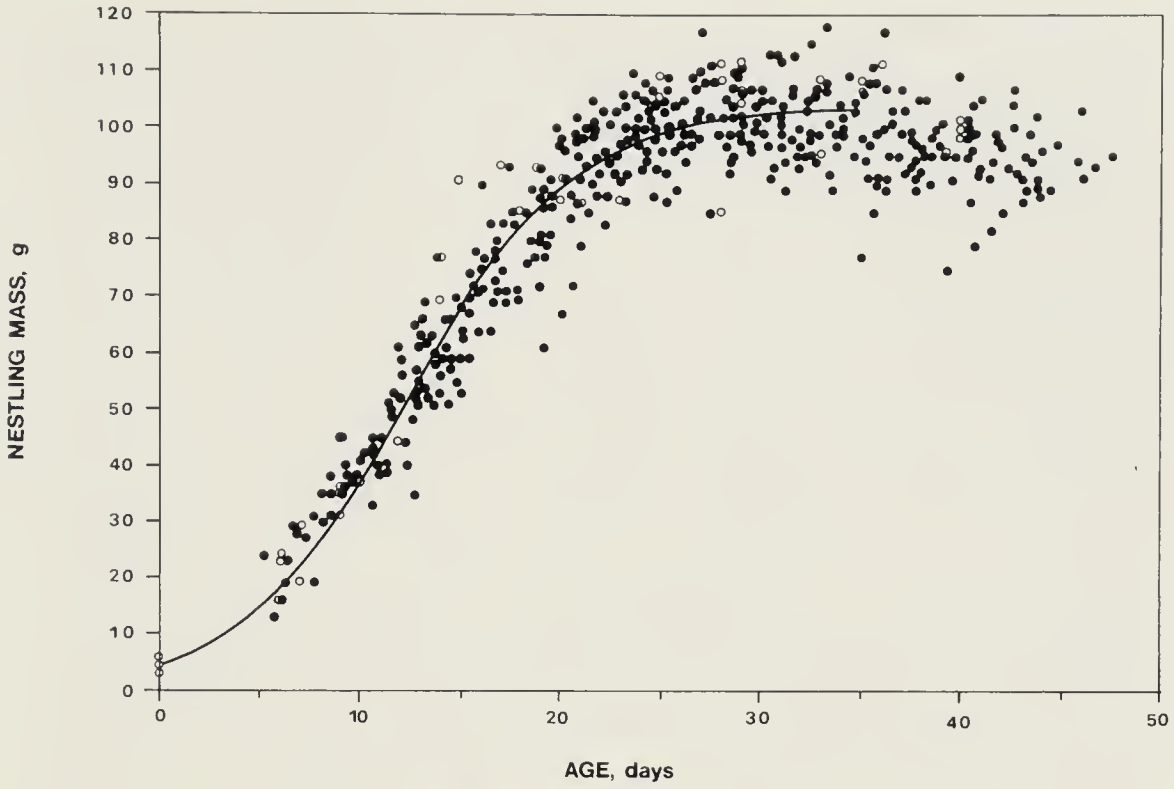

FIG. 1. Mass as a function of age in Monk Parakeets. The logistic curve was plotted using the parameters corresponding to the pooled data from three years. Solid circles show the observed successive masses of the birds whose age at first weighing was calculated by using the curve equation. Open circles represent the weights of eleven nestlings of known age.

Our K (0.2437) is higher by about 50% than that observed by Caccamise and Alexandro (1976) and Caccamise (1980) in captive bred Monk Parakeets. Consequently, the time required to grow between 10 and 90% of the asymptote (T_{10-90}) is in our case 9 days shorter than the 26.98 days determined by these authors. The difference between their K and ours is much greater than the maximum value of 30% observed in other species of birds for populations of the same subspecies in different localities (Ricklefs 1968). Unfortunately, we cannot assert if we are dealing with a different subspecies, since Caccamise and Alexandro (1976) and Caccamise (1980) do not mention the subspecies which they studied. On the other hand, there seem to be close similarities between their parakeets and ours since there are no significant differences in the dimensions of the eggs or in the average mass at laying (6.3 ± 0.56 g, $N = 419$), and there is also a great coincidence in the fledging age. However, adults in our case are 11.8% heavier than those used by Weathers and Caccamise (1978), and the same difference exists in the peak weight of nestlings. This is a noteworthy fact since our subspecies *M. m. catita* is not the largest within the species (Forshaw 1973), and our adult weight values correspond to the lightest period in the year (Navarro and Bucher in prep.).

We suspect that these discrepancies are not related to subspecific variations, being instead due to differences in diet quality resulting from captive breeding. However, as stated by Bucher (1983) the existence of dietary limits to growth is unestablished and virtually impossible to ascertain. This is one of the reasons why studies carried out under natural conditions are so important (see also Ricklefs 1968).

Given that the hatching of the eggs is asynchronous and considering that the average clutch size is 5.3 ± 1.70 eggs (N = 156), and initial brood size is 4.0 ± 1.71 nestlings (N = 63), the difference in age between the first and the last nestling in an average brood could be around 10 days. This leads to appreciable discrepancies in the sizes of nestlings. To test for differences in the growth pattern among siblings, logistic curves were fitted (iterative method) for two separate groups formed by the first and last hatched nestling from each one of the 23 broods in which both fledged. The oldest nestlings have a higher asymptote and growth rate than the youngest (0.9 and 4.4% higher, respectively). However, *t*-test analyses using standard deviations of jackknife pseudo values for each group revealed no significant differences according to order of hatch (A: $t = 0.474$, df = 44, $P > 0.50$; K: $t = 1.027$, df = 44, $P > 0.20$). In order to detect differences during the early stages of development, we carried out a further test that consisted in making paired comparisons between the percentage of the predicted mass that was achieved in the second weighing opportunity by the two extreme sibs in the brood. The relation (O − E)100/E (where O is the observed second mass and E the predicted second mass from the logistic curve for the respective year) was lower in the youngest nestling in the brood compared to that of its eldest sibling in 14 cases out of a total of 23 (Wilcoxon sign test, $t = 68$, $P < 0.05$).

The lower growth rate of the youngest nestling at an early age is probably due to sibling competition for food that parents bring to the nest. Differences in size decrease in advanced stages of development, thus the young chick achieves a better competitive condition that permits it to increase its growth rate close to that of the first-hatched sib, or even to surpass it when the older members of the brood begin to leave the nest. This has been demonstrated by Stamps et al. (1985) in the Budgerigar (*Melopsittacus undulatus*). Another possibility is that parents in the Monk Parakeet might have feeding behavior strategies which allow control of brood reduction by eventually producing selective starvation of the younger nestlings only when food is scarce (see O'Connor 1978), as reported in the Budgerigar (Stamps et al. 1985).

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Monitoring Galapagos Penguins and Flightless Cormorants in the Galapagos Islands.— Estimating bird population sizes has received much attention and many quantitative methods for analyzing population data have been developed (Ralph and Scott 1981, Seber 1986). However, assumptions implicit in these methods make censuses of some species difficult (Burnham et al. 1980), and replicated censuses which allow statistical testing of abundance patterns may be costly. Increasing the efficiency of census techniques would make replicated censuses more feasible, and if population estimates cannot be acquired due to financial limitations, identification of methods whereby populations could be monitored for major changes in size would be important. For species with restricted ranges, monitoring would be facilitated by identifying areas from which counts could be used to predict the total number that would be counted from a census of the species' entire range. Seber (1986)

FIG. 1. Map of Isabela and Fernandina islands showing the location of the nine zones used in the censuses.

emphasized the need to increase efficiency of census methods. Detecting changes in population size is key to many ecological and management questions and concerns.

Populations of Galapagos Penguins (*Spheniscus mendiculus*) and Flightless Cormorants (*Nannopterum harrisi*) have been censused throughout their range in the Galapagos Islands by systematic counts in all areas where they were believed to occur (Valle and Coulter 1987). Valle and Coulter (1987) described lower numbers after the 1982–1983 El Niño event, but they were unable to test statistically the difference in counts among years because samples

were not replicated. The decline in numbers was readily apparent because of the immediate and high mortality. However, less severe changes in population size could go undetected because of the inability to test the null hypothesis of no change in numbers.

The breeding range of Galapagos Penguins and Flightless Cormorants is limited to <400 km along the coastlines of Fernandina and Isabela, Galapagos Islands, Ecuador (Harris 1974, Boersma 1977). Both species have small populations. In 1986, the adult penguin population was roughly estimated to be 2400 to 4400 birds and the adult cormorants were estimated to number approximately 1000 birds (Rosenberg and Harcourt 1987). These estimates were derived from census data multiplied by a correction factor which was developed from surveys with marked birds (Boersma 1974, C. Valle and M. Coulter unpubl. data.). These censuses were costly and required eight boat days, three boat crew members, and three observers. In this note, we evaluate the accuracy of predicted entire-range-census counts from censuses of sections of the species' entire range. We are not, however, attempting to predict population size, as the accuracy of the counts is not known (Boersma 1977). We assume that the counts are a measure of relative population size.

Methods.—We included censuses from 1970 to 1986 in our analyses. Censuses usually were made from a dinghy with three observers and one boatman, along the coastline of Fernandina and Isabela (Fig. 1). Birds were counted between 6:30 and 17:30 h. Censuses took place between 10 and 200 m from shore; several sites were visited on foot. We used the nine zones (Fig. 1) delineated by Boersma (1977) and recorded numbers of birds in each zone. Adult and juvenile birds were grouped in our analyses because they are often difficult to distinguish in the field.

Data for the 1970 and 1971 censuses were from Boersma (1974, 1977), the 1977 data were from Tindle (unpubl. data), and the 1980–1986 censuses were made by one or more of the authors. Several zones were not covered completely in 1970 and 1971 (Table 1). We combined the penguin censuses done in 1970 and 1971 and used the highest value for a given zone. By treating the two censuses as one, we had counts available for all nine zones. Only four penguins were counted in all years in Zone 9, and <1% of the cormorants were counted in Zone 8; these zones were not included in the analyses for each species, respectively.

We determined the best zone(s) to predict number of birds censused on Isabela and Fernandina and on each island separately, using regression analyses. We performed a series of simple linear regressions to compute a coefficient of determination (R^2) and standard error. We used the total number counted as the response variable and each zone as regressors. Each zone was used separately to evaluate its performance as a predictor variable and a combination of two zones summed was used to evaluate the performance of two zones together. All possible combinations of two zones were evaluated (N = 28). The best predictor was the zone which had the highest coefficient of determination and the lowest standard error of the predicted value of the response variable (i.e., total number counted). We chose these statistics to evaluate zones because we were interested in predicting the total number counted with least bias. We did not use multiple regression analysis because of strong ($r >$ 0.70) correlations among some zones.

We used the correlation coefficient computed above as a measure of the zone's ability to predict total census numbers and correlated that coefficient with the mean percentage of birds counted in each zone. We did this analysis as a way of determining if the number of birds counted in a particular zone was indicative of its ability to predict the total number counted.

Results.—The number of penguins counted increased slightly after a sharp (>70%) decline in 1983 (Table 1). Although there was a precipitous drop in penguins counted from the 1980 to 1983 census (attributed to a major El Niño event, Valle and Coulter 1987), the slight change since then cannot necessarily be attributed to true population fluctuations,

TABLE 1

NUMBER OF GALAPAGOS PENGUINS CENSUSED BY ZONE AND YEAR, 1970–1986

Zone	1970 (Sept)	1971 (Aug)	1970/1971[a]	1980 (Sept)	1983 (Sept)	1984 (Jan)	1984 (Sept)	1985 (Oct)	1986 (Oct)	% of total[d] for all years $\bar{x}$ + SE
1	41[b] (2.6)[c]	381 (19.7)	381 (16.2)	387 (22.1)	86 (21.6)	50 (11.0)	102 (23.4)	134 (20.1)	123 (21.1)	19.4 ± 4.3
2	36 (2.3)	66 (3.4)	66 (2.8)	144 (8.2)	11 (2.8)	21 (4.6)	56 (12.9)	41 (6.2)	23 (3.9)	6.0 ± 3.6
3	83 (5.2)	32 (1.7)	83 (3.5)	151 (8.6)	73 (18.3)	6 (1.3)	22 (5.0)	17 (2.6)	17 (2.9)	6.1 ± 5.9
4	586 (37.0)	281[b] (14.5)	586 (25.0)	260 (14.9)	67 (16.8)	174 (38.0)	68 (15.6)	165 (24.8)	161 (27.6)	23.4 ± 8.3
5	75 (4.7)	15 (<1.0)	75 (3.2)	75 (4.3)	5 (1.2)	10 (2.2)	8 (1.8)	18 (2.7)	37 (6.3)	3.1 ± 1.7
6	144 (9.1)	239 (12.4)	239 (10.2)	201 (11.5)	45 (11.3)	34 (7.4)	59 (13.6)	38 (5.7)	21 (3.6)	9.0 ± 3.6
7	568 (37.0)	619 (32.0)	619 (26.4)	462 (26.4)	93 (23.4)	154 (33.6)	79 (18.2)	232 (34.9)	175 (30.0)	27.6 ± 5.9
8	51[b] (3.2)	298 (15.4)	298 (12.7)	64 (3.7)	18 (4.5)	14 (3.1)	41 (9.4)	20 (3.0)	27 (4.6)	5.8 ± 3.8
9	0 (0)	0 (0)	0 (0)	4 (0.2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	
Total	1584	1931	2347	1748	398	463	435	665	584	

[a] Maximum of 1970 and 1971 census; numbers used in analysis (see text).
[b] Area not completely censused (Boersma 1977).
[c] Values in parentheses are the percent of the total for each year.
[d] 1970 and 1971 not included separately; maximum of 1970 and 1971 censuses included.

TABLE 2

SELECTED RESULTS OF THE REGRESSION ANALYSIS OF THE NUMBER OF GALAPAGOS PENGUINS AND FLIGHTLESS CORMORANTS CENSUSED BY ZONE (SHOWN IN FIG. 1) IN RELATION TO TOTAL NUMBERS COUNTED (F & I) AND TOTAL NUMBERS FOR FERNANDINA (F) AND ISABELA (I) ISLANDS, 1970–1986

Species	Island(s)	Zone(s)	R^2	F	SE
Penguin	F & I	1	0.93	64.7**	227.6
		7	0.98	223.1**	125.8
		1 & 7	0.98	308.1**	107.4
		3 & 7	0.97	197.1**	133.7
		6 & 7	0.99	1127.3**	56.5
	F	1	0.96	125.9**	79.8
		3	0.55	6.2*	272.2
	I	7	0.97	192.1**	70.7
Cormorant	F & I	1	0.71	12.4**	93.6
		7	0.83	24.2**	72.2
		1 & 7	0.87	34.9**	61.7
		3 & 7	0.94	78.4**	42.7
		6 & 7	0.84	27.0**	68.9
	F	1	0.26	3.1*	46.9
		3	0.50	6.9**	38.8
	I	7	0.82	28.4**	48.6

* $P \geq 0.05$.
** $P < 0.05$.

because of the unknown variance due to a lack of replicated censuses. For example, the increase in penguin numbers from September 1983 to January 1984 was probably due to inaccuracies in the census, because the population was unlikely to have increased during a three month period when reproduction was very low (i.e., during the 1982–1983 El Niño, Valle and Coulter 1987).

In all censuses, about 50% of censused penguins were counted along the coastline of Fernandina. More than 70% of the total counted were in zones 1, 4, and 7 (Table 1). Numbers of penguins counted in six of the eight zones (1, 4, 5, 6, 7, 8) were each correlated ($r > 0.86$, $P < 0.05$) with the total penguin count. Zone 7 was the single best predictor (Y = −26.2 + 3.8 [Zone 7]; Table 2). Zones 6 and 7 created the best model for predicting total penguin counts (Y = 11.9 + 2.7 [Zone 6 + Zone 7]). The addition of Zone 6 increased the R^2 to 0.99 and decreased the SE by >50% (Table 2). Zones 1 and 7 were good predictors of the number of penguins counted on Fernandina and Isabela, respectively, with relatively low SE and high correlations (Table 2). The Isabela census numbers were strongly correlated with the Fernandina numbers among years ($r = 0.99$, $P < 0.0001$). Correlation coefficients (of zonal counts to total counts) were not related to the mean proportion of birds counted in each zone ($P > 0.05$).

Number of cormorants counted remained fairly stable until the 50% decline in 1983, which was attributed to the 1982–1983 El Niño event (Valle and Coulter 1987). Since the 1984 census, numbers counted were similar to the pre-1983 counts. Greater than 50% of censused cormorants were counted on Isabela (Table 3). Two of the eight zones were each

TABLE 3

NUMBER OF FLIGHTLESS CORMORANTS CENSUSED BY ZONE AND YEAR, 1977–1986

Zone	1977 (May)	1980 (Aug)	1983 (Sept)	1984 (Jan)	1984 (Sept)	1985 (Oct)	1986 (Oct)	Percent of total for all years $\bar{x} \pm SE$
1	69 (10.1)[a]	129 (15.8)	54 (13.2)	105 (16.5)	149 (17.1)	109 (12.9)	100 (13.4)	14.1 ± 2.5
2	60 (8.6)	32 (3.9)	21 (5.1)	28 (4.4)	15 (1.7)	33 (3.9)	18 (2.4)	4.3 ± 2.2
3	63 (9.2)	65 (8.0)	6 (1.5)	19 (3.0)	58 (6.7)	18 (2.1)	26 (3.5)	4.9 ± 3.1
4	134 (19.6)	82 (10.0)	88 (21.5)	115 (18.0)	99 (11.4)	146 (17.3)	122 (16.3)	16.3 ± 4.2
5	48 (7.0)	209 (25.6)	74 (18.1)	95 (14.9)	191 (22.0)	145 (17.2)	183 (24.5)	18.5 ± 6.4
6	136 (19.9)	102 (12.5)	63 (15.4)	78 (12.2)	73 (8.4)	109 (12.9)	38 (5.1)	12.3 ± 4.7
7	165 (24.2)	181 (22.2)	83 (20.3)	178 (27.9)	271 (31.2)	262 (31.1)	229 (30.6)	26.8 ± 4.5
8	0 (0)	2 (0.2)	2 (0.5)	0 (0)	2 (0.2)	0 (0)	18 (2.4)	0.5 ± 0.9
9	8 (1.2)	14 (1.7)	18 (4.4)	19 (3.0)	11 (1.3)	21 (2.5)	13 (1.7)	2.3 ± 1.1
Total	683	816	409	637	869	843	747	

[a] Values in parentheses are the percent of the total for each year.

correlated with the total numbers counted (Table 2). Zone 7 was the single best predictor of the total cormorants counted (Y = 278.8 + 2.2 [Zone 7]; Table 2). Zones 3 and 7 created the best model for predicting total cormorants counted (Y = 240.0 + 2.0 [Zone 3 + Zone 7]). The addition of Zone 3 increased the R^2 to 0.94 and reduced the SE by 41% (Table 2). Zones 3 and 7 had the greatest predictive power for the number of cormorants counted on Fernandina and Isabela, respectively (Table 2). The Isabela census numbers were marginally correlated with changes in the Fernandina census numbers ($r = 0.73$, $P = 0.06$). Correlation coefficients were not related to the mean proportion of birds counted in each zone ($P > 0.05$).

Discussion.—Most of the zones were good predictors of the total number of penguins counted. However, total number of cormorants counted was only related to zonal counts in two zones. It appears that both populations could be monitored for major changes in size by censusing Zone 7 on Isabela. Including a second zone increased the predictive power of the models. Selection of a second zone to census would depend on the species of interest and logistic support. Inclusion of Zones 6 and 3 would increase the precision of the estimate for penguins and cormorants, respectively. However, if the objectives of the monitoring effort included concerns for populations on both islands, or for comparing changes on islands, then selecting a zone on Fernandina would be appropriate. If concerns about changes in distribution patterns developed, an entire census to reestablish these patterns would be required. Such changes could occur from volcanic activity affecting the coastline, changes in prey distribution, or influence of introduced predators (Barnett and Rudd 1983). It is not clear why some zones are better predictors than others. We would expect number of birds counted in a zone to be important; however, this was not the case. Some zones may lend themselves to less variation simply due to the landscape features that improve visibility. In order to reduce potential sources of error, the census should take place within definable limits of sea conditions, search time, and a standard number of observers.

The strong correlation between penguin numbers from Isabela and Fernandina census counts and the weaker correlation between cormorant numbers on these two islands may be due to the greater mobility of penguins and restricted movements of cormorants. Harris (1979) found cormorants were faithful to a location and found only one that was banded on Fernandina and later sighted on Isabela. Boersma (pers. commun.) found that 6 of 234 adult penguins moved >50 km. This suggests that the cormorant population would be more affected than penguins by a demographic change on any one of the islands. Monitoring the population on both islands may be desirable.

Delineating census zones and correlating numbers counted in each zone with the total number counted enabled us to identify areas where bird counts fluctuated most consistently with the total number counted. Our results suggest that censuses over a portion of a species' range can predict the total number that would be counted. Replicate counts in these zone(s) would enable total-number counts to be estimated and would allow a quantitative evaluation of population-size changes to be made. This method allows censuses of species that have restricted ranges to be more efficiently monitored. Changes can be evaluated more accurately if the census effort is directed more to replicated counts rather than to entire-range counts.

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Female-female aggression in White-tailed Ptarmigan and Willow Ptarmigan during the pre-incubation period.—Aggression among female birds usually is less conspicuous than among males. Focus on female behavior, however, has revealed that female-female aggression is directed toward defense of space (Herzog and Boag 1977), nest sites (Gowaty 1981, Leffelaar and Robertson 1985), and/or mates (Jenkins 1961, Yasukawa and Searcy 1982, Petrie 1986, Hobson and Sealy 1989) and may be critical in shaping the social system. More specifically, active monopolization of mates by females was hypothesized by Wittenberger and Tilson (1980) to be a factor that could maintain a monogamous mating system. Monogamy is the predominant mating system for both White-tailed Ptarmigan (*Lagopus leucurus*) and Willow Ptarmigan (*L. lagopus*) (Wittenberger 1978). In both species, males accompany females almost constantly until onset of incubation. White-tailed Ptarmigan males remain with the hen through early and mid-incubation, accompanying her when she is off the nest. Once the eggs hatch, the male plays no part in brood rearing, contrary to the Willow Ptarmigan where males remain with broods until autumn (Wittenberger 1978). Aggressive interactions between female ptarmigan have been observed during the breeding season, principally before the onset of incubation. MacDonald (1970) and Hannon (1983)

showed that paired female Rock Ptarmigan (*L. mutus*) and Willow Ptarmigan, respectively, threatened and/or attacked "intruding" models of females during spring. Whether this aggression was for the purpose of defending a territory or monopolizing a mate was not determined. Regardless, males would have a more difficult time acquiring second mates. Hannon (1984) suggested that territorial hen ptarmigan prevent potential secondary hens from settling on the same site in spring, and thus a monogamous pairbond is maintained by female-female aggression. If this hypothesis is to provide a general explanation for the maintenance of monogamy in ptarmigan, one would predict similar levels of female-female aggression in other populations of Willow Ptarmigan and in the two other closely related ptarmigan species. The purpose of this study was to examine levels of female-female aggression during the preincubation period in other ptarmigan populations. We presented female models to female White-tailed Ptarmigan in Colorado and to Willow Ptarmigan in Manitoba. We also reexamined Hannon's data for Willow Ptarmigan in British Columbia, and report relevant data from a Rock Ptarmigan study in Nouveau Québec.

Study areas and methods.—Models were presented to female ptarmigan from mid May to early June, after pairing and before laying. Presentations, by Lord and Martin, to female White-tailed Ptarmigan were at Mt. Evans and Loveland Pass, Colorado (CO) in 1987 and 1989. Presentations in 1986 by Martin were to female Willow Ptermigan at LePérouse Bay (LPB), Manitoba. Hannon's 1980–82 presentations were at Chilkat Pass (CP), British Columbia and were described earlier (Hannon 1983).

We set a model of a hen ptarmigan in breeding plumage and in semi-alert posture within 20 m of a hen and guided the female toward it until we were sure she could see the model. We then moved away, waited 5 min, and recorded her behavior for 10 min (5 min by Hannon). As a control, Hannon presented a stuffed female Bufflehead (*Bucephala albeola*) at CP, and Lord and Martin used a milk carton; both controls were similar in size to ptarmigan but did not resemble either a conspecific or a potential predator. No control was used by Martin at LPB. Models were presented once to each hen. We recorded whether females ignored or approached the model or control, the closeness of the approach, and the number of attacks and vocalizations (territorial and aggressive calls). To test for independence of behavioral responses between populations, sampled randomization tests (N = 500) were used (Sokal and Rohlf 1981), and G_{ran} values reported.

Results and discussion.—Responses of females to the female models varied from no response to direct attack and were ranked in order of increasing intensity from 1 to 4 (Table 1). The three populations of female ptarmigan differed in their responses to the models (G_{ran} = 36.97, df = 6, $P < 0.0001$). This heterogeneity was due to differences in responses both between and within species. White-tailed Ptarmigan females (CO) were less aggressive to the models than Willow Ptarmigan hens (CP and LPB combined) (G_{ran} = 28.39, df = 3, $P < 0.001$). Female Willow Ptarmigan were less aggressive in Manitoba (LPB) than in British Columbia (CP) (G_{ran} = 8.57, df = 3, $P = 0.05$). The proportion of hens that vocalized (territorial or threat calls) to the models varied among the three populations: 19% of 27 hens at CO, 59% of 17 hens at LPB, and 96% of 23 hens at CP vocalized (G_{ran} = 35.01, df = 2, $P < 0.001$). Most hens did not respond to control models, and hens with a rank = 2 did not vocalize or approach closely (Table 1). Female Willow Ptarmigan at CP were more responsive to the ptarmigan model than to the duck model (G_{ran} = 20.73, df = 3, $P < 0.0001$). Female White-tailed Ptarmigan also did not respond in any obvious manner to the control model, but since only five of 27 hens approached the ptarmigan model closely, the responses of the CO hens did not differ between the female and control model presentations (G_{ran} = 6.76, df = 3, $P = 0.11$).

Response to the ptarmigan model did not vary among age classes of female in any population. At CO, 14 adult hens had a mean response of 1.9 ± 0.3 [SE] while 10 yearling

TABLE 1

RESPONSES OF FEMALE PTARMIGAN TO FEMALE MODEL PRESENTATIONS[a]

Model	Rank of female response[b]				
	1	2	3	4	N
L. leucurus (CO)	12 (44.5)	10 (37)	3 (11)	2 (7.5)	27
Control (CO)	11 (79)	3 (21)	0 (0)	0 (0)	14
L. lagopus (LPB)	2 (12)	4 (24)	9 (53)	2 (12)	17
L. lagopus (CP)	0 (0)	2 (9)	11 (48)	10 (43)	23
Control (CP)	3 (60)	2 (40)	0 (0)	0 (0)	5

[a] N = total number of presentations; numbers in parentheses are the percentages of females giving a certain response.
[b] 1 = no response, bird continues to feed, preen, or sit as she had been doing previous to our approach, no alert posture; 2 = approach to >1 m but less than 10 m, female in semi-alert or alert posture; 3 = approach to <1 m, often circles model in alert posture; 4 = attack.

hens had a mean rank of 1.8 ± 0.3 (t = 0.15, df = 22, ns). At LPB, five adult hens had a mean response of 2.2 ± 0.4, while two yearling females had a mean rank of 3.0 ± 0.0 (t = 1.3, df = 5, ns). At CP, 14 adult females had a mean response of 3.4 ± 0.2, and seven yearling hens had a mean rank of 3.3 ± 0.3 (t = 0.26, df = 19, ns).

We observed natural aggressive encounters, involving chases and threats, between neighboring monogamous and co-resident polygamous Willow Ptarmigan hens at both LPB and CP, although less frequently at LPB. Encounters between White-tailed Ptarmigan females are rare during the pre-incubation period (Schmidt 1988, C. E. Braun pers. comm.). During 1987 and 1989, we observed only one natural encounter at CO between two polygamous hens; the dispute, involving a chase and "flight screams" (Schmidt 1988), was short and was terminated when their mate escorted one of the hens away. Thus, with natural observations and by using model presentations, we have observed a similar repertoire of female aggressive behaviors for the three ptarmigan populations. However, the frequency and intensity of these aggressive behaviors varied within populations and between species.

Variation in the extent to which resources such as food, territory, or mates are limiting could explain the differences in levels of female-female aggression we observed among the three populations. For instance, Jenkins (1961) reported increased agonistic interactions among female Gray Partridges (*Perdix perdix*) when numbers of mates were limited. Unmated males occur in most ptarmigan populations (Braun and Rogers 1971, Hannon 1983, Martin 1984, Olpinski 1986, Brodsky and Montgomerie 1987). Hence, levels of female-female aggression likely are not explained by shortages of males in these species. However, there may be shortages of quality males or territories, and this, as yet, has not been tested.

Another potential factor influencing aggression is breeding density. Densities (breeding pairs/km^2) at the time of the model presentations were: CO 1.6, LPB 10, CP 40–50. Thus, observed levels of female aggression were higher with increased breeding density. Levels of aggression tend to increase with increased densities in other species (Moss and Watson 1980, Krebs 1985). In some male birds, testosterone levels, which are related directly to levels of aggression, increase directly with encounter rates (Wingfield 1989). Whether this occurs in females is unknown. Ptarmigan populations fluctuate in density over time. Breeding pairs per square kilometer have varied at CO from 0.8 to 4.6 (Braun and Rogers 1971, C. E. Braun pers. comm.), at LPB from 5 to 10 (Hannon et al. 1988), and at CP from 20 to 50 (Hannon et al. 1988). It would be useful to continue these presentations over several years and look for relationships between density and levels of aggression within populations. In

particular we would like to examine levels of female–female aggression in a population of White-tailed Ptarmigan where densities are comparable to those observed for Willow Ptarmigan at LPB.

Finally, our results may reveal differences in levels of female-female aggression between the ptarmigan species that may or may not relate to differences in breeding density. In a population of Rock Ptarmigan in Nouveau Québec with breeding densities of 8.5–9.8 pairs/km^2, Olpinski (1986) observed no aggression by females towards a hen model in a total of 50 trials during and after pairbonding. However, on Bathurst Island, MacDonald (1970) observed a hen Rock Ptarmigan attack a female model; densities were not reported for this study. Neither of the above studies reported instances of natural aggressive encounters between females. Hence, female Willow Ptarmigan may use overt aggression to exclude other females from their territory or their mate, as suggested by Hannon (1983, 1984). White-tailed Ptarmigan and Rock Ptarmigan females may rely on other behaviors, or encounters may be so infrequent that female-female aggression is not a prominent part of their behavioral repertoire during the pre-incubation period.

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Comparison of activities within families and pairs of wintering Canada Geese.—Canada Geese (*Branta canadensis*) have strong family bonds and social hierarchies. Interactions within and among families of geese and dominance relationships have been described in many earlier studies (e.g., Raveling 1969, 1970; Prevett and MacInnes 1980; Lamprecht 1986; Black and Owen 1989b). Few studies have examined the effect of such social structure on the allocation of time among activities, such as foraging, resting, and vigilance. These studies usually have addressed parental investment during the breeding season (Lazarus and Inglis 1978, Giroux et al. 1986, Eberhardt et al. 1989). Most families remain intact through the winter (Elder and Elder 1949, Sherwood 1967, Raveling 1969), and adults may continue protective parental behaviors such as vigilance and defense of young. The allocation of time and energy by parental adults and their offspring in winter and the impact of parental investment on their activity budgets have not been adequately described. Extensive marking of Canada Geese in the Mississippi Flyway with neck bands (Sullivan et al. 1989) provided

the opportunity to compare activity budgets of wintering Canada Geese of known age, sex, and family affiliation. This study describes the differences in diurnal activities between adults and their offspring and between adults in pairs within four periods of the non-breeding season.

Study area and methods.—Neck-banded Canada Geese were observed from October through March, 1983–1987, near Swan Lake National Wildlife Refuge, Missouri, a traditional migration and wintering area. Observations were conducted where marked pairs and families were present. Observations were random relative to time of day and reflected the distribution of geese among habitats, which changed seasonally (Austin 1988). Marked individuals of pairs and families were observed for ≥15 minutes to determine differences in activities. Activities of two or more marked individuals in a pair or family were recorded simultaneously every 15 seconds using a 15–60× spotting scope and metronome (Wiens et al. 1970, Altmann 1974). Activities were classified into the following categories (McKinney 1965, 1969): (1) sleep (bill is tucked under wing); (2) loaf (head and neck are reclined on the back); (3) preen; (4) comfort (stretch, shake, or scratch); (5) feed (including all feeding modes such as digging, dabbling, and tipping up); (6) locomotion (swim and walk); (7) high alert (where the neck is stretched upward to full length); and (8) low alert (where the neck is upright but relaxed). Age and sex of individual birds were determined from neck band codes and banding records. Family or pair status was determined by the behavior of marked individuals toward other geese (Raveling 1970) and close association with other marked geese.

Observations were divided among four periods each year, based on conditions recorded locally: (1) early fall (October, during early migration, mild temperatures, and prior to hunting season); (2) late fall (November to freeze-up [which occurred when mean temperatures were <0°C for five or more days], and including the hunting season); (3) winter (freeze-up period); and (4) spring (final thaw, starting when mean temperatures were >7°C for four or more days). For each observation session, the percentage of time spent in each activity was determined for each individual. Differences in time spent in each activity between an adult male and adult female in a pair or between an adult and a juvenile in a family group were determined for each observation session. Within each seasonal period, these differences were tested using Wilcoxon signed-rank tests (Conover 1980), pooling observations from all years and habitat types. These tests were based on differences between two individuals during simultaneous observation sessions rather than based on means between two groups. Because each set of birds was observed simultaneously, variability due to habitat type and environmental factors such as disturbances and weather was eliminated. The influence of family size on activities was not evaluated because of difficulties in accurately identifying total family size in many cases. Habitat type and family size and interaction between these factors may influence activities (Gregoire 1985, Lamprecht 1986, Black and Owen 1989b); however, pooling of observations from different habitats and of all family observations may minimize these potential effects on activities.

Results.—Juveniles and adult males within families differed fairly consistently in their allocation of time to feeding and vigilance (alert behavior) (Table 1). I did not test differences in winter because of the small number of simultaneous observations; however, differences were similar to those in other periods. Juveniles allocated significantly more time to feeding than did adult males in fall and spring. Adult males spent more time at high alert than their offspring in all periods and at low alert in spring. Total time spent alert (low and high alert combined) was significantly higher in adult males in late fall and spring. Adult males and juveniles in families were similar in the time spent in other activities ($P > 0.10$). Similar differences are apparent in the comparisons between adult females and juveniles (Table 1), although only feeding activity in late fall could be statistically tested. In late fall and winter,

TABLE 1

AVERAGE DIFFERENCES ($\bar{x} \pm$ SE) IN THE PERCENTAGE OF TIME SPENT IN VARIOUS ACTIVITIES BY WINTERING CANADA GEESE IN FAMILIES AND PAIRS IN THE SWAN LAKE AREA, 1983–1987

		Families										Pairs				
		Adult males vs juveniles					Adult females vs juveniles					Adult males vs adult females				
Season	Activity	(N)	(h)	$\bar{x}$	SE	P^a	(N)	(h)	$\bar{x}$	SE	P	(N)	(h)	$\bar{x}$	SE	P
Early fall	Sleep	(6)	(5.7)	−6.0	4.7		(0)	(0)				(24)	(30.1)	1.8	5.9	
	Loaf			5.5	5.6									−9.7	5.8	
	Preen			3.5	3.4									5.7	1.6	***
	Locomotion			0.1	0									−0.2	1.1	
	Comfort			−0.2	0.2									0.3	0.2	
	Feed			−0.6	5.4									−1.4	2.3	
	High alert			9.6	4.0	**								1.6	1.6	
	Low alert			2.6	7.4									0	1.8	
	Total alert			12.2	7.6									1.6	1.8	
Late fall	Sleep	(22)	(18.5)	3.3	3.9		(6)	(5.2)	−1.4	2.5		(22)	(20.9)	−2.0	3.2	
	Loaf			−0.9	1.3				2.7	2.2				−5.3	2.4	***
	Preen			−3.4	1.9				0.2	0.6				−1.3	1.8	
	Locomotion			−1.5	1.3				−1.4	0.9				−0.5	0.8	**
	Comfort			−0.4	0.3				0.3	0.2				0.1	0.3	
	Feed			−14.1	4.5	**			−7.7	5.8	**			−0.8	3.4	
	High alert			14.6	2.9	***			10.2	5.1				2.2	1.3	
	Low alert			1.0	4.3				−2.1	2.8				3.9	2.3	
	Total alert			15.6	6.0	***			8.1	6.0				6.1	2.8	

TABLE 1
CONTINUED

Season	Activity	Families										Pairs				
		Adult males vs juveniles					Adult females vs juveniles					Adult males vs adult females				
		(N)	(h)	x̄	SE	P[a]	(N)	(h)	x̄	SE	P	(N)	(h)	x̄	SE	P
Winter	Sleep	(4)	(3.0)	−12.2	5.9		(3)	(3.5)	3.1	0.7		(23)	(24.1)	5.4	4.6	*
	Loaf			6.8	4.0				−0.7	1.2				−5.6	4.4	
	Preen			1.3	1.5				0.6	1.2				1.6	1.3	
	Locomotion			0.3	0.7				0	0				0	0.9	
	Comfort			0	0.4				0.5	0.7				−0.2	0.2	
	Feed			−7.3	7.3				−16.3	8.6				−6.5	2.9	***
	High alert			7.2	6.0				16.0	9.3				4.8	1.5	***
	Low alert			2.4	2.2				0.4	1.9				4.6	2.0	**
	Total alert			9.6	4.5				16.4	7.6				9.4	2.1	***
Spring	Sleep	(9)	(9.0)	−2.3	7.0		(0)	(0)				(17)	(14.2)	−3.5	2.1	**
	Loaf			0.9	2.0									3.6	2.9	
	Preen			1.3	1.4									−1.6	1.8	
	Locomotion			−1.6	1.2									0.5	0.5	
	Comfort			0	0.8									1.1	1.0	
	Feed			−21.3	8.5	**								−4.8	2.6	
	High alert			8.6	3.2	**								2.0	1.4	
	Low alert			10.0	6.8	*								1.4	1.9	
	Total alert			18.6	5.8	**								3.4	2.1	

[a] * $P \leq 0.10$, ** $P < 0.05$, *** $P < 0.01$.

adult females spent less time feeding than juveniles and appeared to spend more time at high alert and in total time alert.

Differences in some activities occurred between paired adult males and females in each period (Table 1). Females spent significantly more time than their mates moving and loafing in late fall and sleeping in spring. Males devoted significantly more time than females to preening in early fall and sleeping in winter, but spent less time feeding in winter. Vigilance varied little between members of a pair except in winter, when males spent significantly more time at high alert and low alert. Differences in total time alert were also significant.

Discussion.—The consistent differences in time spent foraging and vigilant behavior between adult males and their offspring suggest a trade-off between time allocated to the two activities and behavioral costs for continued parental care in the non-breeding season. In wintering Barnacle Geese (*B. leucopsis*) (Black and Owen 1989a) and Lesser Snow Geese (*Anser caerulescens*) (Gregoire 1985), feeding time of parents appeared to be restricted because they devoted more time than non-parental pairs to vigilance and aggression. High vigilance and low foraging time of adults with young also were reported for Snow Geese on the breeding ground (Giroux et al. 1986). The actual cost to the parent (less time available for foraging or maintenance activities), however, may not be significant enough to affect the parent's body condition or survival. Vigilant parents may compensate for less foraging time by increasing their efficiency or intensity of feeding (e.g., food finding or peck rate). Also, Black and Owen (1989a) suggested that continued association of parents with their offspring in spring may increase the parents' chance of breeding in the future due to a "contributor effect," where goslings in the family contribute to vigilance and family defense. This would allow greater foraging time for parents and help minimize the cost of parental care.

The behavioral costs to the parent of increased vigilance may be balanced by benefits to their offspring and future fitness (i.e., better survival of its offspring through the non-breeding season). Vigilance of adult geese acts to maintain family cohesiveness, such as in flight initiation, and in the defense of food patches or family members. Because adult males with families are highest in the social hierarchy of the flock (Raveling 1969, Prevett and MacInnes 1980), vigilance of adult males may reduce the need for juveniles' vigilance and also enhance the foraging opportunities of their offspring through agonistic behavior in defense of food resources (Raveling 1970, Lazarus and Inglis 1978, Scott 1980, Gregoire 1985). In wintering Barnacle Geese, goslings in families grazed for longer periods and were less frequently victims of intraspecific aggression than unattached goslings (Black and Owen 1989a). In Greater Snow Geese (*Chen caerulescens atlantica*) on spring staging areas, lone juveniles spent more time searching and walking and less time foraging than juveniles with families (Turcotte and Bedard 1989). The increased foraging opportunities for juveniles with families may thus result in better levels of nutrition and energy reserves, as indicated for wintering Barnacle Geese (Black and Owen 1989a), and, in turn, in better survival or health during stresses encountered during migration and winter. In ducks, lipid reserves have been related to ability to survive inclement weather (Bennett and Bolen 1978, Whyte and Bolen 1984) and the hunting season (Haramis et al. 1986, Hepp et al. 1986).

Although behavioral trade-offs are less apparent between paired adults, the increased vigilance of males in some periods also may be related to future fitness consequences. As described above for their offspring, vigilance and protection by dominant adult males may enhance survival and foraging opportunities for their mates. Male Canada Geese spent more time vigilant and less time feeding than their mates in winter when environmental conditions were most severe. Lack of differences of vigilance and feeding time in the other periods of this study may be related to the low power of the tests, more moderate environmental conditions relative to winter, and, in late fall, to the higher level of disturbances due to the hunting season.

In spring, enhanced foraging opportunities may be particularly important for adult females because of their reliance on lipid reserves for reproduction (Raveling and Lumsden 1977, Aldrich and Raveling 1983). In both parental and non-parental pairs of wintering Barnacle Geese, males spent less time feeding than their mates, and parental males also spent more time vigilant (Black and Owen 1989a). However, migrant Canada Geese do not begin spring deposition of lipid reserves in preparation for breeding while in Missouri (Austin 1988). Differences in spring foraging and vigilance between mates may be more marked on northern staging areas.

Simultaneous observations of wintering Canada Geese in families and pairs suggest a trade-off between vigilance and feeding. Whether the general patterns reported here differ among habitats, family size, time of day, or later into spring is unknown. Although the data are insufficient for specific hypothesis testing, the results provide preliminary information for further investigations. The interactions within and among families of geese are complex and warrant more detailed examination to understand better family social systems, allocation of time and energy, and parental investments. More thorough studies of the activities and parental investment of nonbreeding geese should evaluate multiple factors, including habitat type, family size, dominance or agonistic behaviors, season, body condition, survival, and future fitness for breeding activity.

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"Foot-quivering" as a foraging maneuver among migrating *Catharus* thrushes.—We have observed a foraging technique ("foot-quivering") among *Catharus* thrushes that, heretofore, had been described only as an aggressive display used during intraspecific encounters. Foot-stirring or paddling behavior has been observed among foraging waders, gulls, and shorebirds

and presumably functions to bring invertebrates to the surface of the substrate (e.g., Rand 1956, Meyerriecks 1959, Hoyt 1961, Simmons 1961, Goss-Custard 1969, Pienkowski 1983). Among North American thrushes, analogous behavior has never been reported during foraging, although the Wood Thrush (*Hylocichla mustelina*) and the *Catharus* thrushes are all ground-foraging birds whose feeding behavior has been studied during the breeding and wintering seasons (Willis 1966, Paszkowski 1984, Holmes and Robinson 1988). Dilger (1956a, b) observed "foot-quivering" during hostile, intraspecific encounters on the breeding grounds, and Willis (1966) regarded "foot-quivering" as hostile behavior among wintering and transient thrushes in South America. We describe the behavior and suggest that "foot-quivering" as a foraging maneuver functions to flush prey.

The narrow woodlands (cheniers) along the Louisiana coast and the wooded barrier islands along the Florida, Alabama, and Mississippi Gulf coasts are important stopover sites for Nearctic-Neotropical passerine migrants following spring trans-Gulf migration (Moore and Kerlinger 1987). The Peveto Woods study site (29°45′N, 93°37′W) is a 3-ha coastal woodland located in Cameron Parish, Louisiana. The woodland supports a vegetation cover that includes tooth-ache tree (*Zanthoxylum clava*) and live oak (*Quercus virginiana*) but is dominated by hackberry (*Celtus laevigata*). Foraging observations were made in an area where the understory had been removed and the grass was mowed (approximately 10 cm high).

Observations of ground-foraging thrushes were made throughout the daylight hours between 06:30 and 18:00 CST in April 1988. Behavior of foraging individuals was continuously recorded during observation periods that averaged 104 sec for Gray-cheeked (*C. minimus*) and Swainson's (*C. ustulatus*) thrushes and 75 sec for Veerys (*C. fuscescens*). The frequency of occurrence and duration of "foot-quivering" were recorded for each individual during that time period. We also quantified the rate and pattern (orientation) of foraging movements by: (1) estimating the distance (m) moved while hopping or walking on the ground, (2) recording the number of pauses and feeding attempts, and (3) estimating the direction of movement with reference to the previous movement.

The distinctive feature of "foot-quivering" was a rapid movement of the legs and feet against the substrate without forward locomotion. The bird's neck and head were stretched forward while the bill was held parallel to the ground. After a bout of "foot-quivering," the bird scanned the substrate, presumably searching for prey that might move. "Foot-quivering" was often followed by quick pecking motions directed forward and at the ground. We sometimes observed prey flushed and captured by a foraging thrush at this time. After a bout of "foot-quivering," a thrush continued to hop or walk forward relative to its previous movement, which moved the bird over unsearched ground and decreased the likelihood of path recrossing (see Smith 1974).

Wood Thrushes were never observed to "foot-quiver" while foraging during stopover ($N = 103$), whereas all three *Catharus* thrushes were equally likely to employ this maneuver ($\chi^2 = 0.87$, $P > 0.05$) while ground foraging (Table 1). When the maneuver was observed, it occurred 4 times/min regardless of species. Although the average rate of "foot-quivering" movement varied among the three species (Table 1), the differences are not statistically significant (one-way ANOVA, $F = 0.88$, $P > 0.05$). "Foot-quivering" was followed by pecking movements (prey attacks) 60% of the time among Veerys, 67% in Gray-cheeked Thrushes, and 70% of the time among Swainson's Thrushes. Pecking rates were essentially the same among species and were comparable to those recorded when individuals were not observed "foot-quivering" (Table 1).

Although we do not question previous interpretations that regard "foot-quivering" as a hostile (intraspecific) display, the context in which "foot-quivering" occurred during our study and the frequent attempts to capture prey that followed the movements indicate that the behavior functioned to flush prey. Further, aggressive encounters were not observed

TABLE 1

QUANTITATIVE DESCRIPTION OF "FOOT-QUIVERING" AS A FORAGING MANEUVER AMONG *CATHARUS* THRUSHES DURING MIGRATORY STOPOVER

Species	% Foraging observations (N)[a]	Quiver rate[b]	Maneuver rate[c]	Pecking rate[d]	
				With	Without
Gray-cheeked Thrush	43 (90)	64 ± 14	4 ± 2	5 ± 2	5 ± 5
Swainson's Thrush	38 (56)	54 ± 15	4 ± 2	5 ± 3	4 ± 3
Veery	35 (48)	69 ± 13	5 ± 2	5 ± 2	4 ± 2

[a] Percentage of total number of foraging observations when maneuver observed.
[b] Mean ± one SD rate of foot-movements per min.
[c] Mean ± one SD frequency of maneuver per min.
[d] Mean ± one SD pecking rate per min with and without "foot-quivering."

among foraging thrushes employing this behavior, the behavior was always observed in a foraging context, and we never observed a response to "foot-quivering" by neighboring thrushes, although we cannot rule out a latent effect (i.e., "foot-quivering" may subtly maintain individual distance) and solitary thrushes showed the behavior.

Why "foot-quivering" as a foraging maneuver has not been observed outside of migration may be a function of sample size. The high number of individuals that concentrate at stopover sites following trans-Gulf migration and actively forage to replenish depleted energy reserves increases the likelihood the maneuver would be observed. Further, because acquiring enough food to meet energy requirements is an important constraint during migration, the appearance of "foot-quivering" during migration may represent an expansion of an individual's feeding repertoire. Alternatively, the expansion of habitat-use characteristic of the migration period may precipitate a corresponding change in the use of habitat-specific behavior.

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A nonparametric aid in identifying sex of cryptically dimorphic birds.—Discriminant function analyses (DFA) have been used to sex birds from external morphometric characters (e.g., Shugart 1977, Ryder 1978, Rising and Shields 1980, Wooller and Dunlop 1981, Hanners and Patton 1985, Blohm 1987, Edwards and Kochert 1987). In some species, subtle nonmetric plumage characters may aid in sexing hand-held birds, but their inclusion in discriminant function models statistically is inappropriate. Here we present an alternative method (multiple logistic regression, MLR) for sexing birds based upon suites of morphometric and categorical plumage characteristics. We apply the method to a sample of White-throated Sparrows (*Zonotrichia albicollis*), a species difficult to sex based upon external characters outside the breeding season. MLR relates a dichotomous dependent variable (sex in this case) to several explanatory variables (i.e., morphological characters) (Harrell 1986). MLR has the advantage over other classification algorithms, such as discriminant function analysis (DFA), since its use is appropriate when assumptions of multivariate normality are violated (Press and Wilson 1978). Thus, it is possible to include categorical and dummy variables as explanatory variables. A step-wise procedure can be employed whereby a morphological variable is included in the regression model if its significance is less than a critical value (e.g., 0.05) and is removed if its significance falls above a critical value (e.g., 0.10) in order to identify those morphological characters most important in differentiating the sexes. The probability (P) of a specimen's belonging to a group (in this case the probability of a bird's being male, $Y = 1$) is then $P(Y = 1) = 1/(1 + \exp(-L_x))$ where L_x is the logistic function. The fraction of concordant pairs of observations (c) indicates the predictive ability of the model and is a better indicator than the percentage of correctly classified cases (Harrell 1986). This concordance is calculated by pairing all observations with different values of the dependent variable (Y) and then counting the number of cases where the individual with the larger Y has a higher estimated P than the individual with the smaller Y. Ties are counted

as one-half rather than given a full rank of one (Harrell 1986). Since DFA and MLR give similar results when samples are normally distributed and covariance matrices are equal (Neff and Marcus 1980), the predictive ability of DFA and MLR can be compared indirectly by examining the fraction of concordance of MLR models containing only wing length and those containing wing length and categorical variables.

In order to examine the utility of MLR in sexing the cryptically dimorphic White-throated Sparrow, we measured wing-chord length and five plumage characters of 462 museum specimens (302 males and 160 females) and 40 live specimens (25 males and 15 females). The White-throated Sparrow demonstrates a range of plumage characteristics in both males and females (Lowther 1961, Thorneycroft 1975), and there apparently is a relationship between sex, size, and morph (Rising and Shields 1980). During the non-breeding season, when cloacal protuberance and brood patch are not available as indicators of sex, determining sex of hand-held birds generally is by wing chord length (Atkinson and Ralph 1980, North American Bird Banding Manual 1984, Watt 1986). Males and females demonstrate considerable overlap in size, however, and there is disagreement as to the extent of this overlap (Atkinson and Ralph 1980, North American Bird Banding Manual 1984). Due to evidence for clinal variation in morphology (Lowther 1961), we restricted our measurements to birds collected in the eastern United States and Canada, from South Carolina north to Newfoundland and west to West Virginia. Only birds of known sex with a right wing chord free of feather damage or tip wear were included in the sample, and wing chord length was measured to the nearest mm. Museum specimens were assumed to be sexed correctly. Birds in juvenal plumage (here designated as juveniles) were excluded from the analysis. Live birds were measured at the time of capture and sexed later by laporotomy.

Plumage scores were adapted from Lowther (1961), Vardy (1971), Atkinson and Ralph (1980), and Watt (1986). Birds were considered white-striped (WS) or tan-striped (TS) based on the color of the median crown-stripe. Lateral stripes were scored as all black (B), mixed black and brown (BBr), or all brown (Br). A single crown-stripe value was then assigned to each bird based on the increased presence of brown feathering on both median and lateral stripes (i.e., WS/B = 1, WS/BBr = 2, WS/Br = 3, TS/B = 4, TS/BBr = 5, and TS/Br = 6). Superciliary stripe color was assigned values of: (1) no apparent yellow, (2) small dull yellow stripe, (3) large dull yellow stripe, or (4) large bright yellow stripe. Throat lines (malar marks) were assigned values of 1 to 5 as illustrated by Lowther (1961). An index of throat patch brightness was modified to reflect the contrast of throat color with chest color and extent of streaking of the chest: (1) a dull gray streaked throat with no contrast with the streaked breast, (2) a dull gray non-streaked throat with slight but apparent contrast with the streaked breast, (3) a fully white throat and complete contrast with a light gray breast without a marginal border of black feathering, and (4) a fully white throat separated from a fully dark gray breast by a discrete bordering of black feathers. These five categorical characters were chosen since they are easily and rapidly scored under field conditions (see Watt 1986). All measurements were performed by BAS in order to eliminate variance associated with multiple participants (Nisbet et al. 1970). For the logistic regression procedure, we chose entry and retention criteria of $P < 0.05$ and $P < 0.10$, respectively.

Mean wing chord length (±1 SD) of males (N = 327) was 73.3 mm ± 2.1 and of females (N = 175) was 69.8 mm ± 2.4 and differed statistically between sexes ($t = 16.95$, $P < 0.0001$). Few males (<5%) had wing chord lengths of less than 70 mm, while few females (<8%) had wing chord lengths >73 mm (Table 1). In this sample, >80% of birds at each wing chord length <71 mm or >73 mm were females and males, respectively. The greatest area of overlap occurred at 71 and 72 mm, where roughly half of all birds were of either sex.

Two variables (wing length and throat lines) entered and were retained in the following

TABLE 1

PERCENTAGES OF MALE AND FEMALE WHITE-THROATED SPARROWS AT EACH MEASURED WING-CHORD LENGTH AND THE PERCENTAGE OF MALES IN THE SAMPLE[a]

Wing length (mm)	Females (%)	Males (%)	All birds (% male)
62	0.57	0.00	0.0
66	2.29	0.00	0.0
67	13.70	0.92	6.3
68	13.70	2.80	16.7
69	20.60	1.83	8.2
70	17.70	3.67	17.2
71	8.60	8.56	50.0
72	7.40	10.10	57.7
73	7.40	22.00	74.8
74	3.40	18.70	84.5
75	2.30	20.50	90.0
76	1.10	7.30	86.6
77	1.10	3.40	74.7
78	0.00	0.31	100.0

[a] N = 502.

stepwise logistic regression model ($\chi^2 = 215.03$, $P < 0.0001$): $L_x = -41.10 + 0.59$ wing length $- 0.28$ throat lines. The fraction of concordance for this model was 0.87, whereas with only wing length in the model c was 0.86. Similarly, wing length combined with crown-stripe color also resulted in a model with predictive ability ($\chi^2 = 213.03$, $P < 0.0001$). Thus, $L_x = -37.88 + 0.60$ wing length $- 0.54$ crown stripe. The fraction of concordance again was 0.87 with both variables in the model.

White-throated Sparrows demonstrate seasonal and age-related differences in plumage characteristics (Atkinson and Ralph 1980) and also may experience wear on primary feathers affecting the use of these characters to identify sex. Accordingly, we divided our sample into summer and winter samples. Birds collected from May through July comprised a summer sample (N = 161), while birds collected from October through March comprised a winter sample (N = 167). This regrouping did not appreciably affect either model. The model which included wing length and throat lines had a c of 0.84 for winter birds. With only wing length considered, the model for winter birds had a c of 0.83 and for summer birds a c of 0.90. Throat lines did not enter the model for summer birds.

The North American Bird Banding Manual (1984) recommends that White-throated Sparrows with wing lengths ≤67 mm be classified as females and that those birds with wing lengths ≥74 mm be classified as males. Atkinson and Ralph (1980) found that all birds with wing-chord lengths >72 mm were males and those with wing lengths <68 mm were females. In our study, one-half of all birds with wing-chord lengths of 71 or 72 mm were either male or female. When MLR was applied to this sample, throat lines alone entered the model ($\chi^2 = 5.22$, $P < 0.05$), but this model had a modest fraction of concordance ($c = 0.66$).

In this study, we combined a continuous metric variable (wing chord length) with several categorical plumage variables in an effort to predict sex of White-throated Sparrows. The

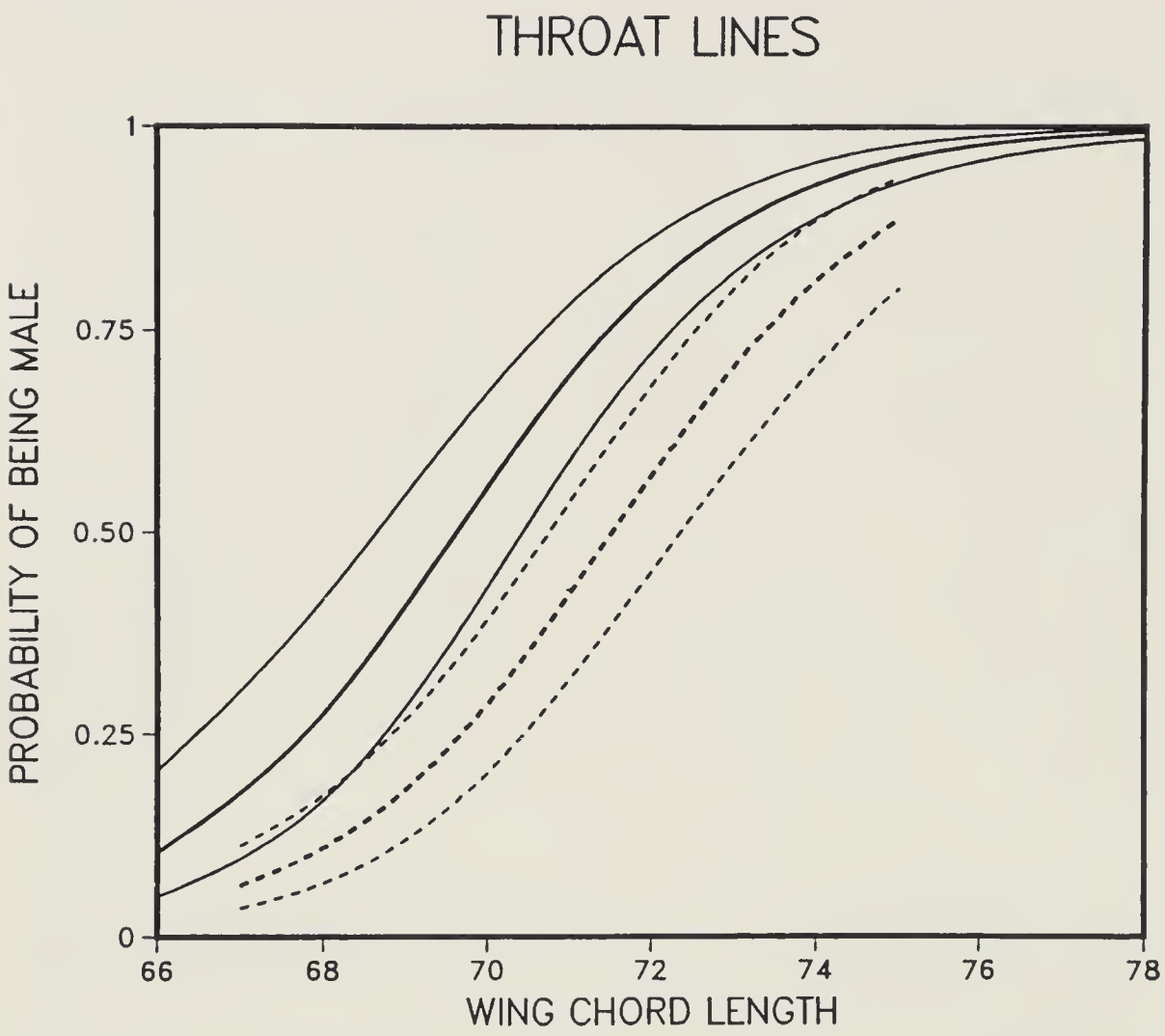

FIG. 1. Probability curves derived from a multiple logistic regression model of wing length and throat lines. The solid lines represent throat line values of one and the dashed lines represent throat line values of five. Both probability curves (thick lines) are bounded by 95% confidence limits (thinner lines). We included values for each curve only within the range of wing lengths observed in this study. The form of the probability curves of wing chord length and crown-stripe color are similar and are not illustrated.

logistic regression model supported the supposition that males were larger than females. Two related characters (crown-stripe color and throat lines) contributed to the predictive strength of the resulting models, thereby increasing the number of individuals in the sample which could be sexed accurately. However, the improvement in classification over wing length alone was slight. Nevertheless, the increased presence of brown feathering on median and lateral crown stripes or increased number and darkening of throat lines moved the probability curve to the right (Fig. 1), thereby decreasing the region of overlap between sexes. Similarly, the shift in the probability curve to the left by the presence of a white median crown stripe together with increased black feathering on lateral crown stripes or a lack of throat lines increased the probability of an individual's being a male. The improvement in classification was greatest for birds of intermediate size where wing-chord length alone was useless for determining sex. While we included only one continuous variable in

our analysis, the use of other continuous variables (e.g., tarsal length or beak dimensions) may enhance the predictive ability of logistic regression models.

Categorical plumage variables contributed a high degree of statistical significance to the MLR models. In practical terms, however, these plumage variables provided only a modest gain in the ability to sex White-throated Sparrows accurately, although it is possible that predictive ability may be improved if birds could be segregated by age or status of their molt or if additional morphological variables can be included. MLR, using a combination of metric and categorical variables, corroborated previous results for White-throated Sparrows in which only wing length was examined and further substantiated the results of Rising and Shields (1980) in that certain plumage morphs of the White-throated Sparrow may be more specific to one sex than to the other. MLR thus resulted in a slight improvement over other methods (North American Bird Banding Manual recommendation and DFA) of sexing individuals of a species as notoriously difficult to sex outside of the breeding season as the White-throated Sparrow. Although there was still overlap in size and plumage characters between the sexes, the region of uncertainty was reduced by logistic regression. We emphasize that, while MLR resulted in a statistically significant though very modest gain in predictive ability in White-throated Sparrows, application to other species may provide substantial improvement over other traditional (parametric) methods. We suggest that multiple logistic regression may be widely applicable to avian studies where combinations of metric morphological and categorical plumage characters might be useful indicators of sex or taxonomic status. Under conditions of multivariate normality, however, we still recommend the use of DFA since computationally it is more efficient (Efron 1975).

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Brown-headed Cowbird parasitism on Golden-winged and Blue-winged warblers.—The Golden-winged Warbler (*Vermivora chrysoptera*) has been expanding its range northward for about the last 150 years (Gill 1980). It simultaneously has declined and even disappeared in much of its southern range. This pattern has been well documented in, for example, Massachusetts and Connecticut (Gill 1980), southern Michigan (Will 1986), and central New York (Frech and Confer 1987). The decline in southern portions of its range is correlated temporally and spatially with the expansion of a closely related congener, the Blue-winged Warbler (*V. pinus*). Hypotheses that attempt to explain the decline of the Golden-winged Warbler in the south with expansion in the north include the following: (1) Suitable habitat. The Golden-winged Warbler, at least in central New York, nests in successional fields about 20 years old. Reforestation of abandoned farmland occurred about 100–150 years ago in the southern and eastern portions of the recent Golden-winged Warbler range, such as Connecticut and Massachusetts. In the more northern portions of the Golden-winged Warbler range, farmland abandonment occurred more recently and still is occurring. Therefore, large amounts of suitable habitat are still available in the northern expanding portions of the Golden-winged Warbler range. (2) Competition with the Blue-winged Warbler. Expansion of the Blue-winged Warbler into Golden-winged Warbler range is well documented (e.g., Gill 1980, Confer and Knapp 1981, Will 1986). Will (1986) observed that the Blue-winged Warbler dominated the Golden-winged Warbler in central Michigan. However, our observations in Central New York suggested that Golden-winged Warblers dominated Blue-winged Warblers. (3) Expansion of the Brown-headed Cowbird (*Molothrus ater*) into the Golden-winged Warbler range. No sample of significant size has been examined for an effect

TABLE 1

SOURCES OF DATA UTILIZED TO DETERMINE FREQUENCY AND EFFECT OF BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*) PARASITISM ON BLUE-WINGED (*VERMIVORA PINUS*) AND GOLDEN-WINGED (*V. CHRYSOPTERA*) WARBLERS

Name	Nest number	Origin	Dates
WFVZ[a]	345	Eastern U.S.	1870–1940
LONRP[b]	87	Eastern U.S.	1940–1989
T. C. Will	27	Central Michigan	1981–1983
Coker and Confer	9	Central New York	1988–1989
R. L. Scully	6	Eastern New Jersey	1986–1988

[a] Western Foundation of Vertebrate Zoology.
[b] Laboratory of Ornithology Nest Record Program.

of cowbird parasitism on Golden-winged Warbler nesting success. Herein, with historical records from over 400 nests, we test the hypothesis that the Golden-winged Warbler is more susceptible to parasitism by the Brown-headed Cowbird than is the Blue-winged Warbler.

Mayfield (1965) documented that the Brown-headed Cowbird was indigenous to the prairies. Even today, the cowbird remains uncommon or absent in large, unbroken forested areas of the eastern United States such as the Smokey Mountains National Park (Wilcove 1988). Mayfield proposed that birds indigenous to the prairies have had considerable time to develop cowbird defense behavior. Short (1963) provided evidence that by the end of the last glaciation, the Blue-winged Warbler occurred along the prairie-forest ecotone, while the Golden-winged Warbler occurred in the east. Therefore, the Blue-winged Warbler was exposed to cowbird influence for a longer period of time. With the extensive clearing of eastern forests, the cowbird spread east. Mayfield collected nesting data from bird species in each of three regions of the continent: the plains, the prairie-forest ecotone, and the eastern forest. These data weakly supported the contention that birds of the plains had a lower frequency of nest parasitism.

In our study, we have used Blue-winged and Golden-winged warbler nesting data from the following sources (Table 1): our own field work, the Laboratory of Ornithology nest record program (LONRP), a doctoral dissertation by Thomas Will (1986), an extensive study by Robert Scully (in press), and oological data from The Western Foundation of Vertebrate Zoology (WFVZ).

The data from WFVZ show a frequency of cowbird parasitism that is almost identical for the two warbler species (Blue-winged Warbler, 20 of 232; Golden-winged Warbler, 11 of 113; $\chi^2 = 0.20$, df = 1). The chi-square 2 × 2 contingency value is not significant ($P > 0.05$). Data from all other sources for parasitized nests found at any stage of development are likewise not different statistically (Blue-winged Warbler, 14 of 63; Golden-winged Warbler, 15 of 51; $\chi^2 = 0.77$, df = 1). However, the frequency of cowbird parasitism from the older oological data compared to the more recent nest data shows a significantly lower rate of parasitism ($\chi^2 = 20.41$, $P < 0.01$, df = 1). Egg collectors generally did not collect incomplete clutches with cowbird eggs, and this would probably account for most, if not all, of the difference in frequency of reported cowbird parasitism. This collecting preference probably was applied equally to both the Blue-winged Warbler and the Golden-winged Warbler. Excluding data from WFVZ, parasitized nests of Blue-winged and Golden-winged warblers

reached the nestling stage with equal frequency (Blue-winged Warbler, 9 of 47; Golden-winged Warbler, 6 of 39; $\chi^2 = 0.21$, df = 1).

Another measure of the response to cowbird parasitism is the frequency of nest abandonment. We define abandonment as nests observed for two or more visits over a several-day interval with cold eggs and no additions to the clutch. Only a very small sample of such nests was available. For both species, the proportion of parasitized nests that were abandoned was identical (Blue-winged Warbler with cowbird, 2 of 14; Golden-winged Warbler with cowbird, 2 of 14). It is difficult to determine whether abandonment is due to human activity or the presence of the cowbird egg (Rothstein 1975). Theoretically, the observed frequency of abandonment without cowbird parasitism could provide a correction factor for human disturbance, but the sample size is too small to apply this correction with confidence. Yet the limited data do not suggest any difference in abandonment between the Golden-winged Warbler and Blue-winged Warbler.

Much of the preceding data was obtained by single visits to the nests by amateurs. The older oological data is biased against reporting the true frequency of nest parasitism. However, our analyses in all cases involved a comparison between data sets collected by the same procedures, and potential errors are unlikely to have altered the conclusions. Analyses of this large data set suggest that the influence of the Brown-headed Cowbird on both species is very similar.

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A review of bird deaths on barbed-wire fences.—On 4 October 1988 we found a dead adult Eared Grebe (*Podiceps nigricollis*) on a 3-strand barbed-wire fence across a small ephemeral pond in Natrona County, Wyoming. A barb on the lowest wire (about 43 cm above the water) had entangled the bird's skin and undertail coverts. There were no external signs of other trauma. The water level in the pond fluctuates with irrigation returns, and the pond often is dry. Our observation prompted us to review published information on bird collisions with barbed-wire fences (Table 1). Bird injuries and deaths due to fencing have not been reported widely (e.g., Avery et al. 1980). There have been very few reports of bird collisions with fences over water, and we found no other report of an Eared Grebe death on barbed-wire fencing.

Stout (1967), Fitzner (1975), Knight et al. (1980) and Lockman et al. (1987) believed that fences and other man-made objects may be most hazardous for young-of-the-year, migrant, or nomadic birds. Stout and Cornwell (1976) reported that dabbling ducks seem more likely to be involved in collisions with fences and buildings than are diving ducks. Take off and landing, altitude gain, flight speed, and diurnal activity patterns may influence the likelihood of collision with man-made objects for different species (Siegfried 1972, Faanes 1987). We suspect that the hazards of barbed-wire fences over water are greatest for birds that move long distances across the water to take flight or for birds that fly close to the water after taking flight.

Bird collisions with fences probably comprise a very small portion of all non-hunting bird mortality (Stout and Cornwell 1976, Banks 1979, Avery et al. 1980, Jonkers and Smit 1984). An exception could be small populations of birds such as Whooping Cranes (*Grus canadensis*, see Anonymous 1989). However, birds entangled or seriously injured after fence collisions may die of exposure, starvation, drowning, or predation. Their bodies and those of birds killed on fences are likely to be removed quickly by scavengers. Therefore, the full impact of fence-related mortality would be difficult to assess.

We agree with Jonkers and Smit (1984) that preventing bird injuries and deaths on barbed-wire fences (and on other kinds of fences) is ethically important. Preventing bird deaths on fences has not been sufficiently considered for most locations that are managed for birds, or heavily used by them, or for projects with fencing alternatives. Fence construction and fence modification should be a standard consideration in reviewing land management practices or proposed projects. Cornwell and Hochbaum (1971) stated that wire fencing should not be built across water and that unneeded fences should be removed. We suggest that fences across ditches, streams, or rivers, in coves on lakes or ponds, in estuarine areas, or near tall vegetation may be exceptional hazards because they are less likely to be seen by birds attempting to take flight or to land. Hazardous fences should be marked to increase their visibility (Fitzner 1975), replaced by less dangerous fences, or removed, especially in areas used by shorebirds, waterfowl, or cranes. At a minimum, modifications of exceptionally hazardous fences can reduce bird injuries and deaths (Braun et al. 1978).

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TABLE 1
BIRD INJURIES AND DEATHS IN BARBED-WIRE FENCING

Bird species	Location	Reference	Remarks
Eared Grebe (*Podiceps nigricollis*)	Wyoming	This paper	Fence across pond
Great Skua (*Catharacta skua*)	Scotland	Morris (1984)	
Black-headed Gull (*Larus ridibundus*)	Scotland	Morris (1984)	Young birds
Gulls (Laridae)	Netherlands	Jonkers and Smit (1984)	
Sandhill Crane (*Grus canadensis*)	Idaho	Drewien (1973)	
	Idaho	Braun et al. (1978)	
	Oregon	Braun et al. (1978)	
Whooping Crane (*Grus americana*)	Idaho	Drewien (pers. comm.)	
	Colorado	Braun et al. (1978)	
	North Dakota	Anonymous (1984), Drewien (pers. comm.)	Injured, captured
	Western U.S.	Anonymous (1989)	Five of 24 hit fences
Trumpeter Swan (*Cygnus buccinator*)	Wyoming	Lockman et al. (1987), Lockman (pers. comm.)	Fences across creeks
	Western U.S.	Weaver and St. Ores (1974)	
Mute Swan (*Cygnus olor*)	England	Beer and Ogilvie (1972)	Barbed wire under water
Swans (Cygninae)	Netherlands	Jonkers and Smit (1984)	
Canada Goose (*Branta canadensis*)	Unspecified	Williams (1967)	
Geese (Anserinae)	Louisiana	Guillory (1973)	Personal communication
Northern Pintail (*Anas acuta*)	Manitoba	Cornwell and Hochbaum (1971)	Adult male
	Manitoba	Siegfried (1972)	Fence across pond
Cinnamon Teal (*A. cyanoptera*)	Colorado	Stroncek (1978)	Fence across pond(?)
Blue-winged Teal (*A. discors*)	North Dakota	Cornwell and Hochbaum (1971)	Adult male
	Unspecified	Cornwell and Hochbaum (1971)	Nesting female
Lesser Scaup (*Aythya affinis*)	Texas	Krueger and Whyte (1978)	Fence across pond
Ducks (Anatidae)	Louisiana	Guillory (1973)	Personal communication
	Netherlands	Jonkers and Smit (1984)	

TABLE 1
CONTINUED

Bird species	Location	Reference	Remarks
Gray Partridge (*Perdix perdix*)	Oregon	Griepentrog (1929)	
	England	Jenkins (1955)	
Great Blue Heron (*Ardea herodias*)	Colorado	Stroncek (1978)	
	Washington	Knight et al. (1980)	Fence across creek
Grey Heron (*A. cinerea*)	England	Mead et al. (1979)	Eight occurrences
"Blue Heron" (*A. cinerea*?)	England	Jonkers and Smit (1984)	
Least Bittern (*Ixobrychus exilis*)	Louisiana	Guillory (1973)	
Little Bittern (*Ixobrychus minutus*)	Zimbabwe	Irwin (1984)	
Stork (*Ciconia ciconia*)?	Netherlands	Jonkers and Smit (1984)	
Stiltwalkers (Recurvirostridae)	Netherlands	Jonkers and Smit (1984)	
Sora (*Porzana carolina*)	Washington	Knight et al. (1980)	
Clapper rail (*Rallus longirostrus*)	Virginia	Murray (1929)	
Black rail (*Laterallus jamaicensis*)	California	Arnold (1960)	Possible fence strike
American Coot (*Fulica americana*)	Wyoming	PR (pers. obs.)	Adult
Lapwing (*Vanellus vanellus*)	Netherlands	Jonkers and Smit (1984)	
Golden Eagle (*Aquila chrysaetos*)	South Dakota	Walker (1916)	
New Zealand Falcon (*Falco novaeseelandiae*)	New Zealand	Fox (1977)	Female, possible fence strike
Hen Harrier (*Circus cyaneus*)	Scotland	Morris (1984)	
European Kestrel (*Falco tinnunculus*)	Netherlands	Jonkers and Smit (1984)	
	Netherlands	Smit et al. (1987)	
Common Buzzard (*Buteo buteo*)	Netherlands	Jonkers and Smit (1984)	
Common Barn-Owl (*Tyto alba*)	Washington	Knight et al. (1980)	
Grass Owl (*T. capensis*)	Zimbabwe	Irwin and Lorber (1984)	

TABLE 1
CONTINUED

Bird species	Location	Reference	Remarks
Great Horned Owl (*Bubo virginanus*)	Pennsylvania	Edeburn (1973)	Adult male
	Missouri	McCarthy (1973)	
	Texas	Anderson (1977)	
	Montana	GTA (pers. obs.)	
	California	Emerson (1904)	
	Washington	Fitzner (1975)	
	Washington	Knight et al. (1980)	
Spotted Eagle Owl (*B. africanus*)	Zimbabwe	Irwin and Lorber (1984)	
Burrowing Owl (*Athene cunicularia*)	Nebraska	Lohoefener and Ely (1978)	Immature
	New Mexico	PR (pers. obs.)	Released
Short-Eared Owl (*Asio flammeus*)	Washington	Fitzner (1975)	
	Washington	Knight et al. (1980)	
	Scotland	Morris (1984)	
Marsh Owl (*A. capensis*)	Zimbabwe	Irwin and Lorber (1984)	
Great Gray Owl (*Strix nebulosa*)	Manitoba	Nero (1974)	Released, later died
Unspecified owls	Netherlands	Jonkers and Smit (1984)	
Unspecified raptors	England	Weir (1971)	
	Netherlands	Jonkers and Smit (1984)	
Sand Martin (*Riparia riparia*)	England	Mead (1979)	
Dipper (*Cinclus cinclus*)	England	Robson (1969)	Juvenile, fence across stream
American Robin (*Turdus migratorius*)	Oregon	Griepentrog (1929)	
Spotless Starling (*Sturnus unicolor*)	Netherlands	Jonkers and Smit (1984)	

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Wilson Bull., 102(3), 1990, pp. 558–559

Deception in Canada Geese.—Deception in communication and manipulation of one individual by another are relatively new concepts in animal behavior. This note describes how a Canada Goose used the presence of other unrelated geese to obtain access to food. The observation was incidental to a study of Giant Canada Goose (*Branta canadensis maxima*) vocal and visual communication at the Milwaukee County Zoological Park, Milwaukee, Wisconsin. The zoo has a 0.5-ha lake near which I maintained a winter feeding site for my study geese. This site occasionally was used by geese of other subspecies, presumably migrants. Subspecies present 20 February 1982, when the deception observation occurred, were judged by medium size and light color and small size and very dark breast and back color to be Todd's Canada Goose (*B. c. interior*) and the Cackling Canada Goose (*B. c. minima*), respectively. Both subspecies were easily distinguished from my pinioned Giant Canada Geese.

Canada Goose intraspecific aggression has been described (Collias and Jahn, Auk 76:476–509, 1959; Klopman, Beh. 30:287–319, 1968), as has the normal social structure of the geese in winter (Raveling, J. Wildl. Manage. 33:304–318, 1969). Surviving family members normally remain together throughout the winter and often gain access to food via threats and group aggressive displays. Families are effectively closed, usually not tolerating unrelated geese closer than 2–3 m (Raveling, Beh. 37:291–317, 1970). Larger family groups generally displace smaller ones in gaining acccss to food. Single young of the year are subordinate to single adults which are subordinate to pairs; pairs with the most young are the most dominant (Raveling 1969). Lone geese, when approaching a group, almost invariably assume submissive postures, the beak just touching the breast feathers (Klopman 1968) and turn away.

On 20 February 1982, 18–20 Todd's Canada Geese (TCG) and one Cackling Canada Goose (CCG), all flighted, were present near the feeding site. My study geese prevented access to the feeding site as they loafed and fed there from 08:30–11:40 CST. My Giant Canada Geese (CCG) were not a family group but unrelated, wild-caught birds previously confined together in a 5 × 5-m quarantine pen for a month after capture in July, 1981. However, they behaved more like a family than independent yearling geese, demonstrating coordinated behavior in aggressive threat situations. These GCGs prevented access to the corn, even when approached by three and four member families of TCGs in group threat display, and repeatedly repelled the lone Cackling Canada Goose which approached in bent-neck submissive posture.

Just before noon, two adult and six immature TCGs flew into the lake, landing with a greeting ceremony that identified them as a family (Raveling 1969). They swam ashore and without hesitation began walking toward the food. The gander, slightly larger and deeper voiced than the others, approached the food with stiff strides, head down, and neck fully extended, and calling. The remainder of the family followed the gander in line-abreast formation, called, and alternated between neck-pumping (neck extended vertically then brought down to the base with the head touching the breast, often repeated, Klopman 1968) and the horizontal head-neck extension postures of aggression or threat. The Giant Canada Geese quickly ceded the food to the newcomers.

The one thoroughly uncharacteristic act observed during this otherwise normal aggressive displacement was that the lone Cackling Canada Goose, initially displaced by the approaching flock, ran around behind the family and then, neck-pumping and calling, assumed a position in the approaching line. Upon gaining the food pile the family gave a mutual triumph ceremony, waving heads and necks toward one another and calling. The Cackling Canada Goose also called and weaved the neck during this ritual normally reserved for family members, then all settled on their bellies about 0.5 m apart and began feeding. Occasionally the goose on either side of the CCG would stop feeding, rise, and extend the neck in threat toward it. The CCG rose, turned away from the threatening bird and moved off roughly 0.1 m, whereupon the threatening bird would return to feeding. The CCG then returned to feeding also. Several times while the Cackling Canada Goose was feeding, single geese approached the food pile and attempted to displace it via threat postures. When this happened, the family gander chased the approaching goose in head down aggressive posture. The Cackling Canada Goose fed for nearly 25 min before the family gander chased it along with another unmarked single goose which approached and had been attempting to displace the CCG at the food. The lone Cackling Canada Goose, by the deception involved in joining with and behaving as one of the family during the aggressive confrontation and the triumph ceremony, succeeded in gaining access to the food and was protected—as a family member would be—while it fed. The low level of aggression between adjacent family members and the cackler is characteristic of intra-family aggression (Raveling 1970), and the cackler responded as expected for a weak threat between family members. Such a deception has never been reported for Canada Geese. In fact, it has long been accepted that participation in the triumph ceremony is the most reliable means of determining family members from non-family individuals (Raveling 1969). Had the cackler been the same subspecies as the family it joined, I would have assumed that it had simply been separated from and then rejoined its family. The deception would go unnoticed except in marked cohorts or when differing subspecies are involved.

Acknowledgments.—I would like to acknowledge the assistance of the Milwaukee County Zoological Park Director and Administration in making my dissertation study possible and the cooperation of the staff of that institution for their advice and assistance.—PHILIP C. WHITFORD, *Biology Dept., Winona State Univ., Winona, Minnesota 55987.* *Received 30 June 1987, accepted 21 Nov. 1989.*

Wilson Bull., 102(3), 1990, pp. 560–561

A Harpy Eagle successfully captures an adult male red howler monkey.—Harpy eagles (*Harpia harpyja*), the world's largest eagle, inhabit vast, relatively undisturbed lowland Neotropical forests. Skeletal remains of prey found in the vicinities of active nests and sight records indicate that they feed primarily on arboreal mammals (e.g., cebid monkeys, sloths, and procyonids), but occasionally may take terrestrial mammals such as agoutis (*Dasyprocta aguti*) and even fawns of brocket deer (*Mazama americana*: Rettig, Auk 95:629–643, 1978). Here I report a witnessed attack of an adult Harpy Eagle on an unusually large prey, an adult male red howler monkey (*Alouatta seniculus*).

On 22 June 1987, during a faunal survey in Sena Madureira, Acre (9°15'S and 68°39'W), western Brazilian Amazonia, I was travelling in a dugout canoe as we approached a troop of howlers located near the southern bank of the Igarape Xiburema, an 8-m wide forest creek. At 07:22 h, 1.5 h after sunrise, we stopped approximately 45 m downriver from the troop. This group had been involved in a loud dawn chorus for at least 15 min about 20 m above the ground in the upper branches of an emergent tree. We could also hear at least two other neighboring troops counter-calling farther inland. As I was checking the group size and composition, an adult Harpy Eagle attacked the single adult male I could see. The predator appeared rapidly, soaring low over the canopy, and hit the victim which was howling actively, facing the opposite direction, and somewhat peripheral to the rest of the troop. Despite the partial obstruction, I was able to see the commotion in the foliage and hear loud vocalizations and heavy wing-beats. A few seconds later, I could no longer see the victim nor its group-members, which probably fled to lower branches and away from their calling tree. B. Santos, who also witnessed the entire event, saw the raptor carrying an adult male howler in its talons and landing on a lower perch some 30 m away. We assumed that the victim was the only adult male in the group, and that it was killed shortly after the attack since we heard no more stress calls during the next 20 min.

This average-sized male probably weighed about 6.5 kg (mean weight of an adult male howler monkey [Thorington et al., pp. 97–106 *in* Vertebrate ecology in the northern Neotropics (J. F. Eisenberg, ed.), Smithsonian Institution Press, Washington, D.C., 1979]), equivalent to 86% of an adult female Harpy Eagle's 7.6 kg weight (Fowler and Cope, Auk 81:257–273, 1964). Rettig (1978) estimated that a monkey captured by an adult female Harpy Eagle, which "appeared to be half of an adult red howler monkey" of unidentified sex, weighed 6.3 kg, but red howlers were not common prey at the nest he studied (Rettig, in litt.). Adult male red howlers, which are 1.45 times heavier than adult females (Thorington et al. 1979), may be near the upper limit of body mass of arboreal mammals taken by any forest eagle. All other individuals in the group (two or more adult females, one or more subadult males, and one or more juveniles) appeared smaller than the fully grown adult male captured by the raptor. In other surveyed sites of Brazilian Amazonia (Peres, unpubl. data), reliable reports of Harpy Eagles preying on medium-sized primates such as capuchins (*Cebus apella* and *C. albifrons*), sakis (*Pithecia pithecia, P. monachus, P. irrorata* and *P. albicans*), and bearded sakis (*Chiropotes satanas* and *C. albinasus*) are not uncommon. Individual body mass of these primates, however, does not exceed that of howlers. Adult two-toed sloths (*Choloepus didactylus*), which are among the largest prey reported taken by Harpy Eagles (Rettig 1978), also weigh considerably less than adult male red howlers. Considering how little is known about the relationship between avian predators and mammalian prey communities in tropical forests, it is possible that Harpy Eagle predation still exerts strong selective pressure on primate populations.

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the World Wildlife Fund—US. I thank B. Santos for helping me in the field, and N. L. Rettig, C. H. Stinson, and C. R. Blem for critical comments on the manuscript.—CARLOS A. PERES, *Sub-Dept. Vet. Anatomy, Univ. of Cambridge, Cambridge CB2 1QS, England.* *Received 18 Aug. 1987, accepted 17 Jan. 1990.*

Wilson Bull., 102(3), 1990, p. 561

Shiny Cowbird collected in South Carolina: first North American specimen.—On 16 July 1989, a second-year male Shiny Cowbird (*Molothrus bonariensis*) appeared at Hutcheson's bird-feeding station on Sullivan's Island, South Carolina. On 28 July, Post collected the bird (Charleston Museum No. 1989.48). The collection site is in dune habitat (Sea Oats [*Uniola*] and Wax Myrtle [*Myrica cerifera*]) about 200 m from the Atlantic Ocean. The specimen, which pertains to *M. b. minimus,* had the following measurements: weight, 35.2 g; wing chord, 96 mm; tail, 68 mm; tarsus, 26 mm; exposed culmen, 17 mm. The testes were enlarged (left testis = 6 × 3 mm), and the bird was not molting.

The Shiny Cowbird, represented by *M. b. minimus,* has spread rapidly through the West Indies, apparently from the Trinidad-southern Lesser Antilles region (Post and Wiley, Condor 79:119–121, 1977). Although Shiny Cowbirds have been in North America at least since 1985 (Smith and Sprunt, Amer. Birds 41:370–371, 1987), this appears to be the first specimen for North America. It is also the northernmost incursion of the species along the Atlantic coast. We thank John Bull of the American Museum of Natural History for determining the subspecies of the specimen.—WILLIAM H. HUTCHESON, *56 Society Street, Charleston, South Carolina 29401;* AND WILLIAM POST, *Charleston Museum, 360 Meeting Street, Charleston, South Carolina 29403.* *Received 16 Nov. 1989, accepted 18 Dec. 1989.*

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ORNITHOLOGICAL LITERATURE

RAPTORS IN THE MODERN WORLD (Proceedings of the III world conference on birds of prey and owls). Edited by B.-U. Meyburg and R. D. Chancellor, illus. by F. Weick. World Working Group on Birds of Prey, Berlin, West Germany. 1989:611 pp., 64 black-and-white drawings, 273 tables, figs. and maps. $45.00. (Order from W. W. G. B. P., 15b Bolton Gardens, London SW5 0AL, England.)—Despite a title that indicates otherwise, this book represents the proceedings of an international conference attended by 400 participants from five continents, which was held in Eilat, Israel, in March of 1987. As is typical of works of the genre, the book is loosely edited and consists of a compilation of offerings ranging from sketchy abstracts to first-rate research papers. The work is divided into nine parts: Raptors on migration and wintering grounds (19 papers), Population biology and breeding (10 papers), Biology and conservation of rare raptors (14 papers), Biology and conservation of rare owls (10 papers), Raptors in polluted environments (11 papers), Habitat analysis and census techniques (four papers), Promotion of legislation (four papers), Education in raptor conservation (10 abstracts), and Resolutions (10 resolutions passed at the conference). Information concerning the biology and conservation of raptors on six continents is included. Although several of the reports detailing the biology and status of the many "exotic" species discussed were written by indigenous authors, English is the sole language of presentation. Several of the more lengthy papers present important information on the biology of little-known species, while others suggest new insights into the mechanisms affecting the populations of more well-studied raptors. There are a number of useful papers detailing recent conservation efforts. Senner and Brett, for example, offer a reasoned argument for the establishment of a registry of sites of international importance to raptors, and Krupa details the success of the Philippine Eagle (*Pithecophaga jefferyi*) "adopt-a-nest" program in which natives and logging-concession workers are paid to report and then protect occupied eagle nests. Some of the presentations, however, merely summarize already published work, and others would have been better presented in a journal. Indeed, as I read through the proceedings I kept wondering why this disparate collection had not been broken up into logical subunits and published in separate issues of *The Journal of Raptor Research.*

In sum, "Raptors in the modern world" consists of a number of useful papers, some of which when read together could provide a fair overview of the current status of raptor conservation worldwide. There are minor typographical errors throughout the work, but the titled drawings by Friedhelm Weick are exquisite, and the book has an exceptionally appealing layout for a conference proceedings. Because most of the work consists of a series of detailed journal-style papers and lacks a central theme—other than raptor biology in general—I do not recommend that anyone attempt to read the book from cover-to-cover. (I doubt the editors intended the proceedings to be used as such, as they provide no introductory or summary chapters, and no index.) Although individual papers in the proceedings will be of interest to a number of researchers in the field, given its high price, only the most devout raptorphiles will want to acquire the entire work.—KEITH L. BILDSTEIN.

NO WOMAN TENDERFOOT. By Harriet Kofalk. Texas A&M Univ. Press, College Station, Texas. 1989:225 pp., frontispiece, 44 unnumbered text photographs. $19.95.—The subject of this biography, identified in the subtitle "Florence Merriam Bailey, Pioneer Naturalist," was truly a remarkable ornithologist. The bibliography of her writings, included in the book, lists more than 130 articles, a major portion of which were based on her own field work in

what was then the wild and unsettled west. Among the titles are the acclaimed "Handbook of Birds of the Western United States," published in 1902, and the monumental "Birds of New Mexico," which appeared in 1928. Her contributions were recognized by her colleagues who elected her a "Fellow" of the American Ornithologists' Union in 1929 and three years later awarded her its prestigious Brewster Medal.

Although her accomplishments and these honors (she was the first woman to receive them) would be outstanding for anyone, they were particularly noteworthy because Ms. Bailey lived at a time when most believed that women should be educated "solely for womanly purposes, 'in order to be to the man all that he needs' " (p. 9). That Ms. Bailey was subject to discrimination (as defined by present day standards) is clear. She was cited in the 1900 edition of *Who's Who in America* as an author, "the sister of C. Hart Merriam," the noted naturalist and ecologist (p. 103). Whether she reacted to such slights is not clear. The author takes pains to point out that Ms. Bailey purposely took a back seat to her husband, Vernon Bailey, a well known mammalogist, and to her brother. Although she chose to remain quietly in the background, one is tantalized by the contradictory and, by modern standards, feminist remarks that surface in her writings. In perhaps the most revealing quotation in the book, she notes (p. 51), "Like other ladies, the little feathered brides have to bear their husbands' names, however inappropriate. What injustice! Here an innocent creature with an olive-green back and yellowish breast has to go about all her days known as the black-throated blue warbler, just because that happens to describe the dress of her spouse!"

Unfortunately, this issue is not resolved in the book, nor is the contradiction directly addressed. The book details events chronologically, flitting from topic to topic without cohesion. Many worthy subjects, such as Ms. Bailey's role in fighting the use of feathers in the millinery trade and her introduction of ornithology into the public schools of Washington, D.C., go undeveloped. I searched in vain for insights into her independence and her decision to pursue a career unusual for its time and for revelations about the impact of that career and of ornithology on her life. In their place, I found rather saccharine descriptions of birds and nature as inspirations for life. Although Ms. Bailey clearly had a spiritual relationship with nature, I got the impression that to a large degree the author of this book unconsciously had projected her own feelings onto her subject. This is particularly evident in the references to scientific collecting. Ms. Bailey obviously preferred observation to collecting, which she left to others. But she understood the need for the latter and regularly made use of study skins in her writing and her teaching.

Florence Merriam Bailey was a fascinating female ornithologist . Thus, I recommend this book to everyone as an enjoyable introduction to the events of her life and her accomplishments. For an understanding of forces that shaped that life and personality and led to those accomplishments, one will have to look elsewhere.—Mercedes S. Foster.

Helping and Communal Breeding in Birds. By Jerram L. Brown. Princeton Univ. Press, Princeton, New Jersey. 1987:xv + 354 pp, 62 figs., 28 tables, appendix, annotated glossary, indices by author, species and subject. $45 cloth, $16.50 paper.—Dr. Brown tackles a range of issues in evolutionary biology under the rubric of avian cooperative breeding. This kind of social behavior particularly challenges our understanding of evolution because individuals appear to be delaying independent breeding, or allowing their own reproductive potential to be suppressed, to behave parentally toward the offspring of others. The complexity of the issues involved, the jumbled history of different approaches to the issues, and the daunting variety of partially answered empirical questions demand the careful synthetic approach offered by Dr. Brown. It is often tempting to throw up one's hands at evolutionary

issues and the range of approaches that they require, but this book offers hope that even a broad and fundamental issue like the evolution of cooperation can be better understood.

The book is not a text, but it is a lesson in scrupulously reasoned progress in understanding a complex issue. It also provides an education in how amazingly varied birds are in their social lives. Although it appears specialized, the breadth of conceptual issues and depth of empirical testing will excite students of birds, behavioral ecology, and evolution generally. Few other books in evolutionary biology attempt such a synthesis of empiricism and theory while focusing on a central problem. Other books in behavioral ecology that deal at least partly with sociality are either more narrowly focused (often on single species), are more broad reviews without such depth of hypothesis testing, or are collections that can be disconnected and uneven. This book can be used as a guide to basic concepts for students of behavior in general, as well as a thorough reference to empirical studies and interpretation for students of communal birds in particular. In the preface, Brown describes the utility of the book as for those who have not read the extensive original literature. However, the synthetic scope of the book makes it very useful as well for those who have been reading and working in the field; everyone needs to be reminded of the communal goal of synthesis and broad understanding—the development and testing of general principles.

In 18 chapters, Brown takes the reader from a synopsis of the conceptual problem, through a broad empirical and historical review of the study of cooperative breeding, a clear primer of the basic ideas, a breakdown of component issues and clear empirical and theoretical descriptions of them, a tour of the inevitably revealing kinks and variations on the expression of cooperation, to a synthesis of the state of our understanding and overheated disagreements. One chapter, "Elements of inclusive fitness theory for field studies," is a valuable guide for biologists thinking about fitness in societies. A chapter is devoted to the thorough empirical demonstration of the effectiveness of group action ("does helping really benefit the helped?"). A measure of Brown's seriousness about semantic problems is the lengthy justification of the term "communal" breeding in the very useful glossary. The overall structure of the book, and the conclusions sections of each chapter, communicate the author's aim to keep the issues clear and avoid the amorphousness of a summary of a large field that can be suffocating. Dr. Brown is well qualified to do this since he is one of the pioneers in synthesizing results of intensive field work and modern theory in the study of social behavior.

The development of a balanced historical perspective on both empirical and theoretical advances begins in the first chapter aptly titled "Why study helping behavior?" This beginning, including the skepticism about the conceptual importance of cooperative breeding by eminent biologists like David Lack and George Williams, encapsulates the aim of clearly setting out the goals of biologists studying cooperative breeding and identifying their conceptual roots. The lightning rod in this field, and so a focal contention in this book, is the validity of the indirect component of inclusive fitness as a guiding force in the evolution of cooperation. However fundamental this premise may be, and however important its testing, demonstrating the necessity of including indirect selection in an explanation of a system of cooperative breeding would not be itself an explanation. Brown shows that understanding the ecological and demographic forces impinging on individuals is obviously critical to understanding *how* natural selection could favor cooperative traits in an evolutionary game governed by ecological constraints and scored by the tally of genetic copies in future generations. While the heat of the arguments in the literature (and some contentiousness in the book) is generated by the "kin-selection" controversy, the book is an invigorating tour of the arsenal necessary, including especially old-fashioned, careful, determined field work, to resolve such fundamental evolutionary issues.

This book takes on a field that has grown explosively in the last decade. Many long-term studies of ecology and demography of avian populations focus on cooperatively breeding

species. The reason for this growth is that cooperative breeding highlights with particular clarity the potential benefits and drawbacks of sociality to biological fitness. Understanding the evolution of cooperation (quickly defined here as accomplishment facilitated by collaboration) is a fundamental challenge for evolutionary biology. Often only a few of the behavioral parents in communal groups appear to be the genetic parents of young being cared for, raising the question of why nonbreeding collaborators should accept a "helping" role in which reproduction is deferred rather than leave the group to attempt breeding. This kind of breeding arrangement is widespread among tropical birds, although that was not appreciated until the last few decades. Many of the apparently nonbreeding "helpers" (so named by Skutch) are offspring of the adults whose young they are helping to raise; this puts the issue of cooperative breeding in the larger context of understanding conditions under which delayed breeding and philopatry might be favored by natural selection.

One of the book's main accomplishments, really to be found nowhere else, is its broad portrayal of the diverse facts of cooperative breeding—the varied expressions among birds of cooperativeness (including polyandry, polygyny and joint nesting) theoretically united by the potential for indirect selection and delayed direct benefits through communal care of young. Brown develops a classification scheme for 222 species of cooperative birds (in one table!) and his survey of the geographic and taxonomic distribution of known cooperative breeding reveals mainly a trend for greater frequency where permanent residency on territories is common (reinforcing the link to the potential benefits of philopatry) and possibly a link to high survival among small birds in open tropical and subtropical habitats. Later chapters reveal important variation in fundamentals like the genetic constitution of social groups and the frequency of territorial inheritance. Although the details of social behavior, the number of studies presented, and undercurrents of internecine quarrels can weigh on the reader, it is important for students of social evolution to appreciate how varied a seemingly specific phenomenon like cooperative breeding can be; it becomes clear how vain the hope is for a single relatively simple explanation. As Brown says, ". . . when the different types of helper systems are recognized, some of the controversies that have arisen out of semantic confusion are dissipated and real progress on substantive issues is made possible." The book is a benchmark in this progress.—Kerry N. Rabenold.

South American Birds—A Photographic Aid to Identification. By John S. Dunning with collaboration of Robert S. Ridgely. Harrowood Books, Newton Square, Pennsylvania. 1987:351 pp., 1410 color photographs, 2700+ range maps, 4 endpaper maps. $47.50 cloth, $35.00 paper.—This book is a much expanded and improved version of Dunning's 1982 publication, "Land Birds of South America." The new book has approximately 40% more color photos. Although the pictures are smaller than formerly, each now accompanies the pertinent text rather than being grouped on a facing page. The range maps are shaded in color. Best among the editorial improvements is the fact that species accounts (which have been rewritten) are no longer divided into two sections, those with photos and those without. Now plumage descriptions and range maps for all covered species are in one list, whether or not illustrated by a photograph.

Families are mostly listed in accordance with accepted taxonomic practice, the first species being a rhea and the last a finch. However, consistent with Dunning's strong belief that bird identification could be eased for beginners by emphasizing factors other than taxonomy, species and genera are grouped by size and/or habitat. This frequently forces the more experienced birder to use the index to find something he might otherwise turn to directly. Curassows and guans, as "large land birds," come right after rheas, while crakes, dippers, and some sandpipers and plovers are grouped as "small water-edge birds."

Although this book does not deal with pelagic birds or those only likely to be found along ocean beaches, its coverage of more than 90% of South America's almost 3000 species makes it the closest thing to a South American field guide yet available. The descriptions are much easier to use than those in Meyer de Schauensee's "A Guide to the Birds of South America." While the greater detail of Meyer de Schauensee is important, Dunning's book is now an indispensable supplement or it can stand alone. This supremacy is likely to last for some time, for the concise format of Dunning's work will appeal to travelers birding throughout South America even after the massive four volume "The Birds of South America" by Robert Ridgely and Guy Tudor is complete. Just the already available first volume, on Oscines, of this remarkable, high quality set lacks the portability of Dunning's book, which also contains illustrations of a few species not portrayed in the Ridgely/Tudor work.

John Dunning's outstanding bird photography is on display here, although the reproductions, in the review copy at least, do not always do it justice. Some of the pictures are too dark to be really useful and were better in the earlier "South American Land Birds." From my own experience with Dunning's slides, I know that the high quality of his originals is not reflected in some of these illustrations. While this reduces the utility and beauty of the book, it does not seriously compromise its value to amateurs or professionals requiring identification aids for a wide range of species for which no other illustrations exist.

John Dunning devoted the last twenty-five years of his life to obtaining and making available to the public top quality photographs of as many of the bird species of South America as he could find. About 30,000 of his slides are now on deposit with Visual Resources for Ornithology (VIREO), a branch of the Academy of Natural Sciences of Philadelphia. This book contains the cream of the crop. Unfortunately, John did not survive to see the happy result, but the book is a proper tribute to the unlimited time, money, and effort he and his wife, Harriet, put into making it a reality.—WILLIAM BELTON.

THE SPARROWS: A STUDY OF THE GENUS *PASSER*. By J. Denis Summers-Smith, illus. by Robert Gillmor. T. & A. D. Poyser, Ltd., Staffordshire, England; distributed in U.S. by Buteo Books, P.O. Box 481, Vermillion, SD. 1988:342 pp., 8 color plates, 62 black-and-white drawings, 114 numbered maps, graphs, other black-and-white figs., 50 tables. $57.50.—This admirable book is the culmination of a 40-year-long study of the House Sparrow (*Passer domesticus*) and related species. It is a meticulous evolutionary work and the author may justifiably be proud of it. The monograph also offers a wealth of ideas for further work on an interesting and convenient study subject.

The bulk of the book (252 pp.) treats in detail each of the 20 species that Summers-Smith includes in *Passer*. In the first chapter, the five Afrotropical gray-headed species are grouped together, but thereafter each species is discussed in a chapter of its own. These chapters begin with a nomenclature, followed by sections on plumages, biometrics, distribution, habitat, behavior, breeding biology, survival data, molt, voice, and food. These sections vary a good deal in length, depending on how much is known about each species. The author has had field experience with all except the Saxaul Sparrow (*P. ammodendri*) which is scattered in six disjunct populations across physically and politically remote parts of central Asia; his personal knowledge of the sparrows is apparent throughout the book, as is his thorough coverage of the literature (21 pages of references contain about 750 titles) and his wide correspondence with observers within the birds' ranges. The final three chapters discuss characteristics and relationships, origins and evolution, and systematics.

The book ends with two appendices (a seven-page synonomy of *Passer* species and sub-

species and a two-page gazeteer of place names not found in two standard atlases), the references, and a six-page index.

I found the last chapters to be especially interesting, with detailed discussions of why this is such an adaptable, successful, and dynamic group of birds. There is much to be admired in a species such as *P. domesticus,* the "street ragamuffin" that thrives in close associations with man to the degree that it can breed from the tropics to intensely cold climates (some sparrows spend their entire lives in cattle barns in northern Norway, others have survived winters in Churchill, Manitoba, by living in a grain elevator) and that can capitalize on unusual food sources (sparrows are resident *in* London's Heathrow Airport, feeding on cafeteria scraps, and others have been seen feeding 80 stories up on the observation floor of New York City's Empire State Building, *at night*). Perhaps the most famous story of the House Sparrow's remarkable adaptability is based on the birds that lived in a coal mine, 640 m underground, for several years—feeding on miners' handouts and even breeding successfully. Yet this is a species that was early shown to be strongly responsive to photoperiodism!

As the author points out, "divergence within the genus as a whole has been rather small" (p. 253), but perhaps because of this, the birds offer excellent, clear examples of finely tuned adaptation, competition, and interrelationships in their zones of overlap. Summers-Smith argues that *P. domesticus* evolved in the Palearctic and *P. montanus* (the [Eurasian] Tree Sparrow) in the Orient; then they spread into sympatry in the Old World as well as being introduced in recent history into both North America and Australia where their interactions in the zones of overlap are fascinatingly different. Other new sympatries are also discussed, as in southern Africa where *P. domesticus* has been successfully introduced into Cape Sparrow (*P. melanurus*) range but is largely unable to displace the Cape Sparrow in urban areas. The Willow (or Spanish) Sparrow (*P. hispaniolensis*) can live sympatrically with *P. domesticus* in Europe by being an opportunistic, nomadic breeder. In Mediterranean-type climates, *P. hispaniolensis* may breed in one area early in the short, lush spring, when resources are greater than resident *P. domesticus* can exploit. Then *P. hispaniolensis* moves (usually north) for later broods, leaving the long, drier summer to sedentary *P. domesticus.* Yet *P. hispaniolensis* is sedentary and even urban on those islands (e.g., Madeira, the Canaries) where *P. domesticus* and *P. montanus* do not occur.

Summers-Smith offers a well-reasoned and convincingly argued chapter on the sparrows' origins and evolution. He believes that *Passer* originated in the Afrotropical region, and that it has probably attained much of its present distribution in close association with man and his livestock. The author presents a wealth of supporting evidence from paleontology, climatology, and archeology—an unusual addition to an evolutionary ornithology discussion, but possible here because of the sparrows' close association with man.

The final chapter reviews the many morphological, chemical, behavioral, and other taxonomic characters that have been studied in *Passer* species and presents what I think is a reasonable classification for the group.

While reading this book, my only frowns came from the author's use of English names, which I found confusing at times. I grant that the taxonomy and systematics of this genus are difficult, and perhaps Summers-Smith has done as good a job on them as possible, but I found his overreliance on English names jarring, and his emphasis (including vernacular names) on subspecies rather old-fashioned. If *P. motitensis* is the "Rufous Sparrow," even though it has five discrete populations, and three are allopatric or parapatric (*P. m. rufocinctus, shelleyi,* and *cordofanicus*) and given separate names ("Kenya Rufous," "White Nile Rufous," and "Kordofan Rufous" sparrows), why do the ssp. *P. m. motitensis, benguellensis,* and *subsolanus,* which intergrade in southern Africa, all get lumped as "Great Sparrow"? The Cape Verde Rufous Sparrow (*P. iagoensis*) retains full species status and is called the

"Iago Sparrow." I also had a difficult time with "Willow" Sparrow instead of the widely accepted and natural "Spanish" Sparrow for *P. hispaniolensis*; if the English name is to be replaced because the bird is not as common in its type locality of Spain as it is elsewhere, why is *P. flaveolus* called the "Pegu Sparrow" after its type locality in Burma, when it has a broad range over Southeast Asia and might best retain the descriptive, if prosaic, "Plain-backed" Sparrow?

My nomenclatorial quibblings aside, this is an *excellent* book. It is packed with authoritative and detailed information, is outstandingly well written, contains a minimum of jargon, and is almost impeccably literate. The author's style is a joy to read—a statement that few scientific book reviewers can make. This is also a particularly attractive book, neatly done, well designed, and superbly illustrated. Robert Gillmor's color plates are good, but his 62 black-and-white drawings of the birds in various postures and "behaviors," of typical and odd nest sites, and of habitat vignettes make turning the pages a pleasure. The care that went into the writing, illustrating, and production of this book is evidenced by my finding only a single minor error: the town of Modoc, Illinois, is incorrectly spelled on a range map of *P. montanus* but is given correctly in the text. By current market standards, the book is moderately priced. I hope that *The Sparrows* finds the wide readership it deserves.—Mary H. Clench.

Avifaune du Niger: État des Connaissances en 1986. By P. Giraudoux, R. Degauquier, P. J. Jones, J. Weigel, and P. Isenmann. Malimbus, Volume 10, Number 1, June 1988. The West African Ornithological Society. 140 pp., 2 maps, figs., 1 table, 2 appendices. £5 + £1 postage or £2 airmail (Bankers order payable to West African Ornithological Society.)—This work, in French, is a special issue of Malimbus. It consists of a review of the bird fauna of Niger which occupies nearly 1.2 million km^2 in West Africa. The northern part of the country, which comprises about 75% of the area, falls in the desert zone. The authors have recognized and described briefly nine ecological zones that are used throughout the book to define the distribution of each species. A very short history of ornithological work in Niger is provided and one is surprised at how little has appeared in print, as indicated by the short bibliography of 52 titles. Two of the references mentioned in the introduction are not listed in the bibliography. The annotated list makes up the major part of the book and the species sequence is that of W. Serle and G. J. Morel ("A Field Guide to the Birds of West Africa." Collins, London. 1977). For each species (473) the Latin, French, and English names are given along with the status of the species in Niger (Palaearctic migrant, resident, African migrant). The main treatment deals with distribution, including migration dates where applicable. It is divided according to the nine ecological zones described in the introduction and often includes a general summary at the end of each species. In this part, the authors summarize and explain briefly the known changes in distribution and discuss the general status of the species, as well as population trends. The conclusion is interesting in that the authors give a table indicating the origin of the species arranged according to the nine ecological zones they have recognized. They conclude that little is known about birds in Niger and invite whoever travels in this part of Africa to submit their observations to improve the basic ornithological information of this rich but poorly known avifauna. The authors must be congratulated for having compiled the available information and having assembled it in a valuable publication. It is well done and I am sure that it will be useful to anyone travelling in Niger or to whoever needs information about the birds of that country. Such a book should encourage anyone watching birds in this part of Africa to record observations and submit them to the authors.—Henri Ouellet.

THE BIRDS OF GHANA, AN ANNOTATED CHECK-LIST. By Llewellyn Grimes, British Ornithologists' Union, % British Museum (Natural History), sub-department of Ornithology, Tring, Herts HP23 6AP, England. 1987:276 pp., 11 tables, 12 figs., 9 appendices, and 16 habitat photographs. £16.00 UK, £18.00 overseas (add £3.00 for non-sterling payment).—This monograph is No. 9 in the important series of avifaunal check-lists published by the British Ornithologists' Union for various areas of the globe. The regions covered are distant places often in the former and/or present sphere of British influence, and one wonders if North America might be next? The present volume joins Gambia and Nigeria in West African coverage, and Sierra Leone will follow.

Lew Grimes has done splendidly in detailing the knowledge of Ghanaian ornithology and in analyzing and interpreting avifaunal trends and patterns there. This last aspect, presented in tables, appendices, and the Introduction, makes the publication more than an annotated check-list. Nevertheless, the bulk of the book is devoted to short species accounts giving relative abundance, status, habitat, and distribution for each of the 721 bird species found in Ghana. Breeding information is stated for resident birds if known (otherwise, breeding records from other countries in West Africa are presented). The distribution data are documented by literature citations and by names of observers when field notes are the sources of information.

The Introduction is well done and includes sections on political history, ornithological history, geology and topography, climate, vegetational zones, avian breeding patterns, and a comparison of Nigerian and Ghanaian avifaunas. The sections on ornithological history, climate, vegetation, avian breeding and migration are especially informative. The history of ornithology in Ghana starts with a Dutch citizen in 1705 and is traced through a parade of participants, all expatriates, into 1986. Not two or four, but six seasons mark the Ghanaian year, and except for the dry region along the southeastern coast, the coastal third of Ghana is moist forest, the interior is dry woodland and savanna. The various subdivisions of these vegetational zones are carefully described and also shown in photographs. However, I was disappointed not to find a vegetational map of the whole country comparable to the one shown for topography.

The intercontinental migrants wintering or passing through Ghana are called Palaearctic species after the region where they nest. These same kinds of long distance migrants are usually named Neotropical migrants on our side of the Atlantic, thus emphasizing the overwintering location. This difference in terminology probably should be resolved. Forty-six percent of the 229 migrants in Ghana show only intra-African as opposed to intercontinental movements.

Although I understand the reason for naming the observers responsible for bird records reported in the text, I question whether it is necessary. Unlike the literature citations for records included, the primary sources for the formerly unpublished sight records cannot be consulted into perpetuity. Therefore, the book itself should serve as the fundamental source of these bits of information, not the original observers who eventually will depart from our midst. (The only major mistake I noticed was that the legend for Figure 5 on page 24 should have named Table 4, not Table 3. It is stated correctly on page 7.)—DOUGLAS A. JAMES.

BIRDS OF NORTH AMERICA, WESTERN REGION. By John Bull and Edith Bull. Illustrations by James Coe. Macmillan Field Guides, Collier Books, Macmillan Publishing Company, New York, New York. 1989:144 pp., 54 color plates. $12.95 (paperback).—This little book, subtitled "A Quick Identification Guide for All Bird-Watchers," clearly demonstrates the faith of publishing houses that books on birds will sell. Why another field guide? Actually

there is a niche for an inexpensive book that identifies the common birds for the person casually interested in them, and both the authors and the artist have done a competent job of filling that niche. Some 340 of the "most common and conspicuous" birds of the western United States are covered in standard field guide format.

The area covered lies from the eastern borders of the tier of states from North Dakota to Texas, but most of the southern Arizona and southern Texas specialities are omitted. In general I found the selection of species to be somewhat puzzling. Obviously some of the more difficult species have been omitted, but other omissions are less understandable.

For each species the text is a few lines emphasizing identification clues but with a brief statement about expected habitat and a brief outline of the range. The arrangement of species is by color for the passerines and by family group for the non-passerines. The identification comments are adequate for most species but are too brief for some. Unlike other guides of this genre the females of dimorphic species are discussed, but immature plumages usually are not. There is no mention of vocalizations or their use in identification.

On the whole the figures, which are nearer being portraits than simple identification sketches, are well done. For some species there are two figures, but most have only one. Many of the shorebirds do have both a summer and winter plumage figured, but most of the gulls have only the definitive plumage. The illustrations of such toughies as the flycatchers, spotted thrushes and vireos do not greatly help in identification, but the textual clues supplement these. In general the color reproduction leaves much to be desired. For example, the Northern Cardinal (*Cardinalis cardinalis*), Summer Tanager (*Piranga rubra*), Vermilion Flycatcher (*Pyrocephalus rubinus*), House Finch (*Carpodacus mexicanus*), and Purple Finch (*C. purpureus*) are all shown in the same color of red. The blues are somewhat better but subtleties of shade are lacking.

There is a supplemental text chapter which elaborates on the material given in the limited space opposite the figures. There is also a chapter on attracting birds with a list of food plants and hummingbird flowers, as well as standard directions for winter feeding. A brief appendix discusses optical equipment.

In summary this little book will do a fine job of introducing birds to the beginner, but most beginners will soon outgrow it. There is also a companion volume for eastern birds which was never submitted for review.—George A. Hall.

BRIEFLY NOTED

The following publications are available from the Publications Unit, U.S. Fish and Wildlife Service, Room 130, Arlington Square Building, Washington, D.C. 20240.

Techniques for Shipboard Surveys of Marine Birds. By Patrick J. Gould and Douglas J. Forsell. U.S. Fish and Wildlife Service Technical Report 25, 1989:22 pp.—G.A.H.

Program CONTRAST. A general Program for the Analysis of Several Survival or Recovery Rate Estimates. By James E. Hines and John R. Sauer. U.S. Fish and Wildlife Service Technical Report 24, 1989:7 pp.—G.A.H.

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Rondonia Bushbird (*Clytoctantes atrogularis* sp. nov.), a new species of antbird from western Brazil.

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CLYTOCTANTES ATROGULARIS, A NEW SPECIES OF ANTBIRD FROM WESTERN BRAZIL

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ABSTRACT.—A new species of antbird (Formicariidae), *Clytoctantes atrogularis* sp. nov., from eastern Rondônia, Brazil is described and given the English name, Rondonia Bushbird. It is known only from a single female specimen and two sight records of males in terra firme forest near the Rio Jiparaná. The rapid rate of deforestation in Rondônia may present a serious threat to this species. *Received 7 Sept. 1989, accepted 15 May 1990.*

ABSTRACT.—Descrevemos uma nova espécie de Formicariidae, *Clytoctantes atrogularis* sp. nov., do leste de Rondônia, Brasil. A espécie é conhecida sómente por um espécimen (fêmea) é duas observaçôes (machos) em mata do terra firme, cerca do Rio Jiparaná. O rápido desmatamento em Rondônia pousa ameaça de extinçâo a espécie.

The Field Museum of Natural History, in collaboration with the Museu de Zoologia da Universidade de São Paulo, conducted an avifaunal survey of Cachoeira Nazaré along the west bank of the Rio Jiparaná, Rondônia, Brazil (Fig. 1) in 1986 (May, June, July, October, and November). We mist-netted a female of an unusual antbird (Formicariidae), and observed males on two occasions. Subsequent attempts to collect more specimens and observe it further were unsuccessful. Although we are reluctant to describe a new taxon on the basis of a single specimen, the bird's features are so distinctive (see Frontispiece) that we believe it represents an undescribed species. We propose to call it:

Clytoctantes atrogularis sp. nov.

RONDONIA BUSHBIRD

HOLOTYPE.—Museu de Zoologia da Universidade São Paulo 66111 (color slides of prepared specimen on file at FMNH and with the Visual Resources for Ornithology [VIREO]

Division of Birds, Field Museum of Natural History, Roosevelt Rd. at Lake Shore Dr., Chicago, Illinois 60605, U.S.A.

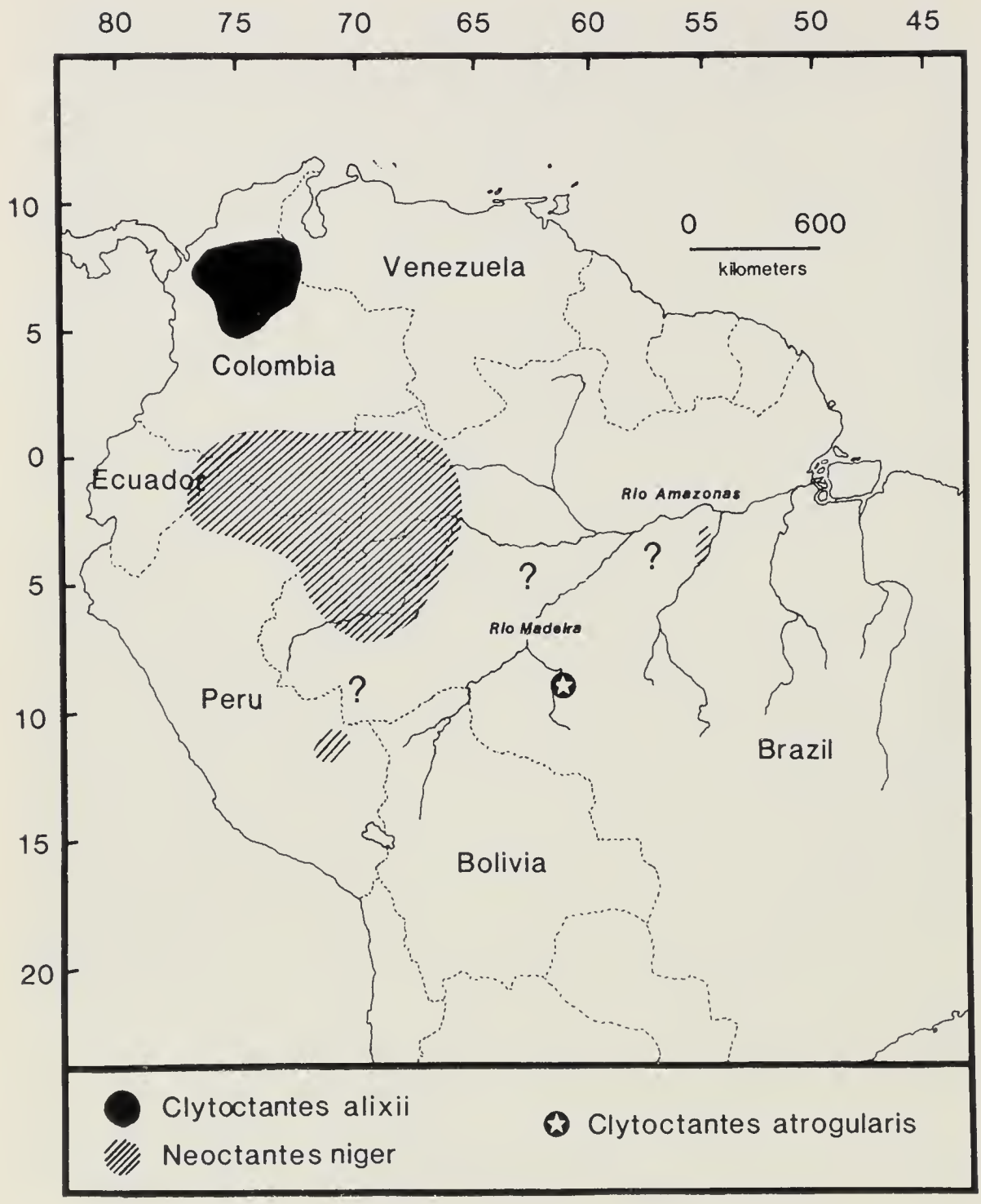

FIG. 1. Known ranges of Bushbirds. Range of *Clytoctantes alixii* taken from Hilty and Brown (1986) and Meyer de Schauensee and Phelps (1978); range of *Neoctantes niger* is from Cory and Hellmayr (1924) and specimen localities known to the authors. Uncertainty about the disjunct nature of the *Neoctantes niger* distribution is indicated by (?).

at the Museum of Natural Sciences in Philadelphia); female (ovaries 5 × 2 mm, ova minute) with fully ossified skull from Cachoeira Nazaré on the west bank of the Rio Jiparaná, Rondônia, Brazil 9°44′S, 61°53′W, elevation 100 m; netted by David Willard on 22 October 1986, prepared by Scott Lanyon, original field number SML86-84.

DIAGNOSIS.—An intermediate sized, sexually dimorphic antbird with a heavy, laterally compressed, all black bill, the mandible of which is sharply upturned. The female plumage is predominantly chestnut with chin, throat, and upper breast jet black. The tail and tail coverts are dark gray. The female is distinguished from female *Clytoctantes alixii* by the black bib, unmarked wing coverts, and dark gray tail coverts. There are no specimens of the male, but sight records indicate that the male is entirely black.

DISTRIBUTION.—Known only from the type locality. However, two independent observations by Ted Parker and by Mort and Phyllis Isler of a male-plumaged *Clytoctantes* at Alta Floresta, Pará, Brazil could be this same species. (See Ecology and Behavior below).

DESCRIPTION OF HOLOTYPE.—The plumage is predominantly chestnut (closest to color 32 [color numbers from Smithe 1975, 1981]). The color changes from dark chestnut on the forecrown, cheeks, crown, nape, and upper back to brown (closest to color 23) on the lower back. There is a concealed white interscapular patch. Upper-tail coverts are gray (closest to color 83) and rectrices are nearly black (closest to color 82). The chin, throat, malars, and extreme upper breast feathers form a jet black (closest to color 89) bib. The bib contains a few scattered chestnut feathers in the malar region. The lower breast, sides, and abdomen are light chestnut. Flank feathers are gray with light chestnut tips. The vent and under-tail coverts are also gray. Upper wing coverts are dark chestnut and unmarked. The remiges are dark grayish brown (closest to color 20) with brown leading edges. The bill is large and laterally compressed (approximately twice as deep as it is wide) and has an upturned mandible. Soft part colors in life: bill, tarsi and feet black, irides dark brown.

MEASUREMENTS OF HOLOTYPE.—Flattened wing 79.0 mm, tail 64.5 mm, culmen length (from anterior edge of nostril) 15.0 mm, culmen length (from base of skull) 25.4 mm, culmen width (at anterior edge of nostril) 4.3 mm, culmen depth (at anterior edge of nostril) 9.5 mm, tarsus 19.5 mm, weight 31.0 g.

ETYMOLOGY.—The specific epithet refers to the black bib of the female.

SPECIMENS EXAMINED.—*Clytoctantes atrogularis*: (MZUSP holotype) from type locality. *C. alixii*: Colombia: Bolívar, Santa Rosa (USNM 4 males, 2 females); Colombia: Córdoba, Quebrada Salvajín, Río Esmeralda (USNM 2 females); Colombia: Antioquia, Puerto Valdivia (AMNH 1 male, 1 female); Colombia: Santander, El Tambor (CM 2 males); Colombia: Cesar, El Cauca (CM 1 male); Colombia: "Bogota" (AMNH 1 male [Type specimen], 1 female): *Neoctantes niger*: Colombia: Putumayo, San Antonio Guamués (FMNH 3 males, 1 female); Colombia: Putumayo, Guascayaco (FMNH 1 male, 1 female); Peru: Loreto, Iquitos (FMNH 1 male, 1 female); Peru: Madre de Dios, Río Palotoa (FMNH 1 female); Brazil: Amazonas, São Paulo de Olivenca, Rio Solimões (CM 1 male); Brazil: Amazonas, Rio Juruá (MZUSP 1 male; SMNH 1 male); Brazil: Pará, Rio Tapajós, Morro do Pau (MZUSP 1 female); Brazil: Pará, Rio Tapajós, Uracagui (MZUSP 1 male); Brazil: Pará, Rio Tapajós, Urucurituba (MZUSP 1 male, 1 female). Locality names follow Paynter and Traylor (1981) and Stephens and Traylor (1983).

REMARKS

Systematic relationships.—Placement within the Formicariidae is supported by the concealed inter-scapular patch and subterminal tomial notch. Within the Formicariidae, only *Clytoctantes* and *Neoctantes* share the unusual bill shape of the new taxon, in which the upper mandibular tomia curve dorsally. When initially described, *Clytoctantes* was distinguished from *Neoctantes* by a difference in bill shape and by its larger feet (with longer claws) (Elliot 1870). These characters were examined to determine

TABLE 1
MENSURAL CHARACTERS OF *CLYTOCTANTES* AND *NEOCTANTES*

	Clytoctantes atrogularis ♀	*Clytoctantes alixii* ♀	*Clytoctantes alixii* ♂	*Neoctantes niger* ♀	*Neoctantes niger* ♂
Culmen width					
$\bar{x} \pm$ SD	4.3	4.00 ± 0.27	4.16 ± 0.23	4.22 ± 0.41	4.29 ± 0.20
(N) range	(1)	(10) 3.7–4.5	(8) 4.0–4.7	(5) 3.9–4.8	(10) 3.9–4.6
Culmen depth					
$\bar{x} \pm$ SD	9.5	8.98 ± 0.32	9.12 ± 0.39	6.96 ± 0.28	7.12 ± 0.29
(N) range	(1)	(10) 8.5–9.6	(6) 8.5–9.5	(5) 6.7–7.3	(10) 6.6–7.6
Culmen length					
$\bar{x} \pm$ SD	15.0	14.89 ± 0.77	15.21 ± 0.71	12.50 ± 0.83	12.86 ± 0.70
(N) range	(1)	(9) 13.7–16.0	(8) 13.9–16.2	(6) 11.4–13.5	(9) 11.8–14.0
Tarsus					
$\bar{x} \pm$ SD	19.5	20.13 ± 0.84	20.22 ± 0.29	20.32 ± 1.83	20.19 ± 2.52
(N) range	(1)	(9) 18.6–21.0	(5) 19.8–20.6	(6) 18.3–20.7	(9) 17.0–24.1
Wing					
$\bar{x} \pm$ SD	79.0	76.8 ± 1.40	78.4 ± 2.19	75.8 ± 3.76	78.8 ± 5.09
(N) range	(1)	(10) 74.5–79.0	(8) 74.5–81.0	(6) 72.0–81.0	(10) 74.0–88.0
Tail					
$\bar{x} \pm$ SD	64.5*	57.44 ± 2.13	59.25 ± 2.87	58.50 ± 4.51	59.4 ± 4.55
(N) range	(1)	(9) 54.0–60.0	(8) 55.0–63.0	(6) 52.0–65.0	(10) 53.0–68.0
Hallux					
$\bar{x} \pm$ SD	17.3*	15.68 ± 0.53	16.15 ± 0.58	12.83 ± 0.61	12.90 ± 0.19
(N) range	(1)	(10) 14.4–16.3	(4) 15.5–19.9	(4) 12.2–13.4	(5) 12.7–13.1
Hallux claw					
$\bar{x} \pm$ SD	9.7	10.33 ± 0.54	10.65 ± 0.47	6.38 ± 0.33	5.96 ± 0.49
(N) range	(1)	(9) 9.6–11.1	(4) 10.2–11.1	(4) 6.0–6.8	(5) 5.2–6.5

* indicates that *Clytoctantes atrogularis* was significantly different from female *Clytoctantes alixii* at $P < 0.05$.
Note the large variability in tarsus, wing, and tail length for both sexes of *Neoctantes*. Specimens from Peru are noticeably smaller than Brazilian specimens. Whether this is the result of a cline or whether the species is polytypic cannot be addressed without specimens from intermediate localities.

the affinities of the new taxon. Hallux length and hallux claw length are significantly larger in *C. atrogularis* than in *N. niger* (Table 1). Hallux length of the new taxon is also significantly larger than in *C. alixii*. Bill size of the new taxon is not discernibly different from that of *C. alixii* but differs significantly from *N. niger* in all three measures (Table 1, see Fig. 2). In addition, the subterminal tomial notch (the notch is used as the homologous point rather than the tip which is subject to wear) is displaced significantly above the horizontal in *C. alixii* and the holotype of *C. atrogularis* but only slightly so in *N. niger* (Fig. 2).

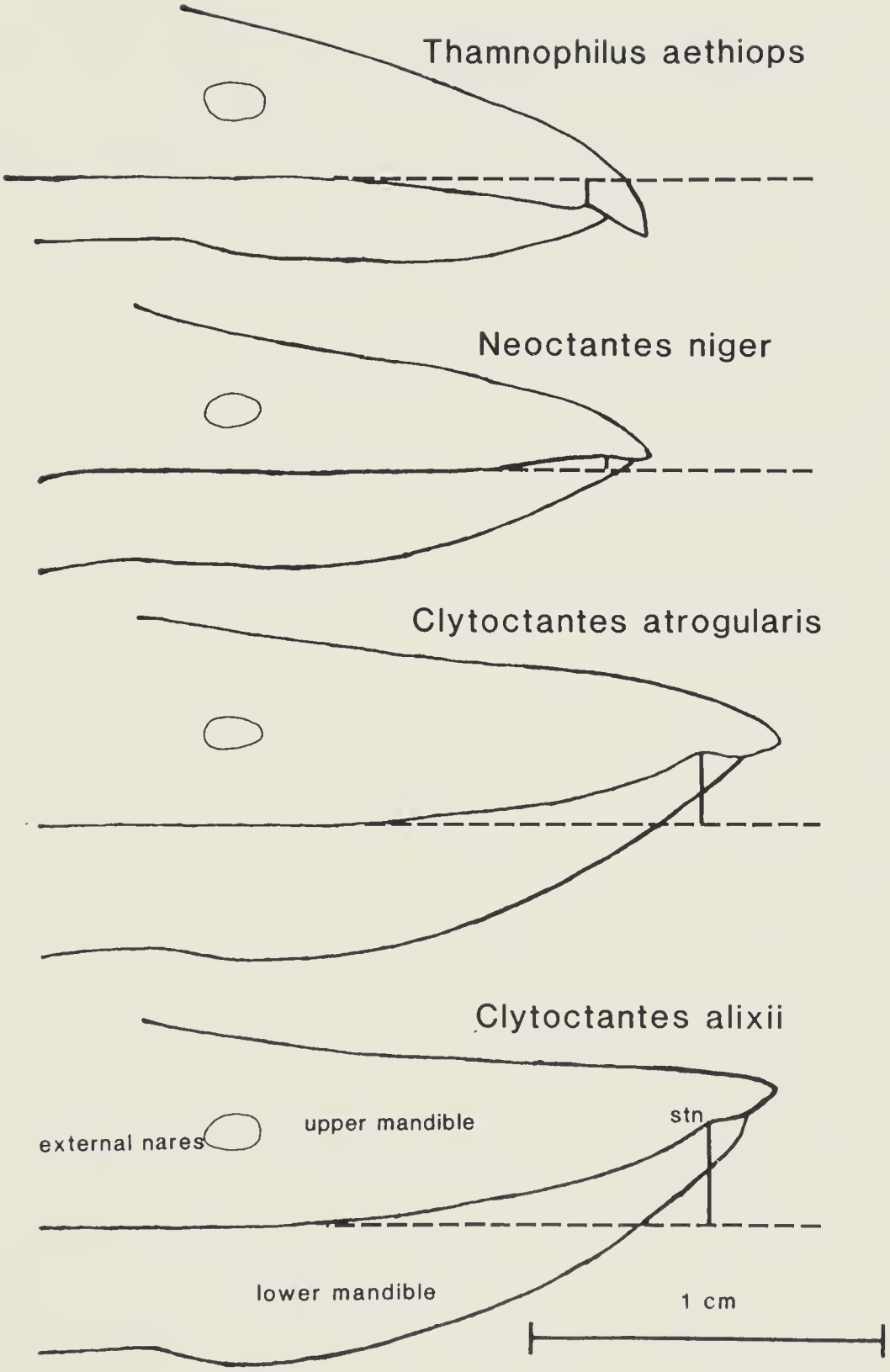

FIG. 2. Bill shape in Bushbirds. Dashed lines are an extrapolation of the line formed by the basal third of the commissure. Vertical lines illustrate the displacement of the subterminal tomial notch (stn) from the horizontal. The typical pattern in the majority of birds is a negative displacement as in *Thamnophilus aethiops*.

Somewhat similar bills have been derived independently within two other suboscine families: the Dendrocolaptidae (*Glyphorhynchus*) and Furnariidae (*Megaxenops, Pygarrhicus, Simoxenops,* and *Xenops*). Although the presence of this character in other families suggests that this bill form could also be mutiply derived *within* the Formicariidae, the strong similarity between the shape and size of the bills of *C. alixii* and *C. atrogularis* suggests that they are similar by common descent.

Plumage coloration is additional evidence that the new taxon belongs in the genus *Clytoctantes.* The adult female collected in Rondônia (sex and skull ossification were confirmed by all three authors) is primarily chestnut like females of *C. alixii,* and unlike the predominantly black female of *N. niger.*

Although *N. niger, C. alixii* and the new taxon probably form a monophyletic group, we prefer to retain the two described genera until the phylogeny of this group can be examined in detail. Bill morphology and plumage characters point to the inclusion of the new taxon in *Clytoctantes,* and it is probably quite closely related to *C. alixii.* With so little known about either *C. alixii* or *atrogularis,* it is difficult to assess just how close this relationship is.

Specific status.—The measurements summarized in Table 1 demonstrate that the holotype of *C. atrogularis* is generally larger than the female *C. alixii* we examined, with tail length significantly greater. *C. atrogularis* has a uniformly black bill but dried specimens of *C. alixii* have pale markings on the bill.

The most obvious differences between these forms, however, lie in plumage patterns and coloration. Five plumage characters differ between the females of *C. atrogularis* and *C. alixii.* The most noticeable difference is the black bib of *C. atrogularis.* There is no suggestion of such a bib in the ten female *C. alixii* examined, all of which have underparts that are uniform chestnut. Male *C. alixii* have a jet black throat and breast (contrasting with the dark neutral gray abdomen and back), but this bib is more extensive than that found in the female of the new taxon. The wing coverts of the holotype of *C. atrogularis* are plain, but in both sexes of *C. alixii* there are wing spots (pale buff in females, black or black with white centers in males). Tail coverts in female *C. alixii* are brown, as is the lower back, while in the female *C. atrogularis* these feathers are dark neutral gray. Rectrices are dark gray in the holotype of *C. atrogularis* and brownish gray in *C. alixii.* The body plumage of the sole specimen of *C. atrogularis* is dark chestnut with the upperparts slightly darker. In *C. alixii* the underparts are slightly brighter chestnut, and this color extends onto the lores and forehead contrasting with the darker and browner crown and back. This contrast is evident in male *C. alixii* as well, where the

forehead and lores are black, like the bib, contrasting with the dark gray crown and back.

These quantitative and qualitative differences, and the 2000 km between known populations of *alixii* and *atrogularis* (Fig. 1), lead us to conclude that: (1) *atrogularis* is not an aberrant *alixii* and (2) that these forms are, and have been, genetically isolated. The observed differences are consistent with levels of differentiation between recognized species in the Formicariidae and lead us to recognize this new taxon as a species. At this time we lack the necessary information to determine whether *C. atrogularis* represents a biological species (sensu Mayr 1969), and additional specimens of *C. atrogularis* are necessary to determine its status as a phylogenetic species (sensu Nelson and Platnick 1981). However, we feel that differences between *alixii* and *atrogularis* are sufficiently great that any additional information and samples will support our recognition of this new taxon as a species, regardless of definition employed.

Description of the male.—The male of *Clytoctantes atrogularis* is known from only two sight records by Stotz (but see Ecology and Behavior below). This bird, or birds, had an all black bill of the shape described for the holotype and its plumage looked to be entirely black in the field. In the absence of male specimens, detailed comparison of male *C. atrogularis* to male *C. alixii* is impossible but the black plumage appeared unlike the dark neutral gray with a black bib of *C. alixii.* The absence of wing spots in the single female specimen suggests that male *C. atrogularis* will also lack the wing spots of male *C. alixii.*

Ecology and behavior.—The holotype was collected from a mist-net set in terra firme forest, dominated by dense vine tangles. The two observations of male-plumaged individuals at the type locality were in the same type of habitat. *C. alixii* also frequents dense tangles in Colombia (Carriker 1955). In the initial 15 min observation on 13 October 1986, the male was approximately 1 m up in a large tree fall and worked up to 2–5 m in a vine tangle. The bird gave a very loud, trilled whistle, "tree-tree-tree," several times at irregular intervals. It was pounding and digging at the vines with its bill. Willis (1988) observed a female *alixii* in eastern Colombia pecking dead stems and ripping gashes in them in much the same fashion. The second brief observation was of a lone individual seen 4 m up in a dense vine tangle.

At Alta Floresta, Rio Teles Pires, Pará in December 1989, Parker and the Islers independently observed a male-plumaged bushbird in dense tangles along a small ravine in terra firme forest. These observers were aware of the finding of a new species of *Clytoctantes* in Rondônia, approximately 500 km to the west, and concluded that they were probably observing this new form. However, the songs from birds at Alta Floresta

were substantially different from those described above from Rondônia. Therefore, whether these Alta Floresta birds represent *C. atrogularis* must be considered speculative until specimens are obtained.

Conservation.—The discovery of this new species is of particular importance in this time of heightened awareness of the uncertain future of tropical forest communities. Although in the past twenty years, more than 25 valid new species of birds have been described from South America, nearly all have been from the Andes and none from Brazilian Amazonia (Mayr and Vuilleumier 1983, Vuilleumier and Mayr 1987). The skewed distribution of new forms reflects not only the distribution of bird species yet to be described, but also the distribution of complete avifaunal surveys. Our discovery of *C. atrogularis* clearly demonstrates that the species composition of lowland Amazonia, like that of the Andes, remains incompletely known. The fact that this distinctive species was observed on only one of two intensive surveys of the type locality and that few such surveys have been conducted in Brazilian Amazonia suggests that additional species remain to be discovered.

At present, *C. atrogularis* is known from only a single locality in Rondônia. Five experienced observers spent 1400 field hours at the type locality and accumulated 1450 net-days. The single netted individual and two sight records suggest that either: (1) this species is extremely uncommon and secretive, or (2) we encountered only dispersing individuals and that it normally occurs in a different habitat. An additional 250 field hours and 375 net-days at a similar locality 70 km distant (but separated by no apparent barrier) resulted in no further observations. If it is indeed endemic to Rondônia, and exists in the low density our experience suggests, then its survival may be seriously threatened by habitat destruction. Rondônia has the fastest rate of deforestation in Brazil (Fearnside 1986). Over 5% of the forest in Rondônia had been destroyed by 1983 (almost all since 1970) and the rate of destruction has increased with the paving of the highway joining Porto Velho to southeastern Brazil in 1984 (Fearnside 1987). Of more immediate consequence, a hydroelectric dam is currently under construction at the type locality of *C. atrogularis*. Unfortunately, our lack of knowledge concerning the habits, habitat requirements, range, and population size of this species limits our ability to make informed recommendations concerning its preservation.

In recognition of Rondônia's high degree of endemism in a number of taxonomic groups (Vanzolini and Williams 1970, Brown 1982, Prance 1982, Cracraft 1985), the scientific community is beginning to focus more attention on this little studied area. With additional work, we may learn enough about *C. atrogularis* to determine whether it is threatened by development of Rondônia, and if so, to formulate plans for its protection.

It seems likely that it occurs in the Reserva Biologica do Jarú which has similar habitat to the type locality, but to date there have been no avifaunal surveys there. We strongly encourage the development of additional parks and reserves in this part of Rondônia to protect not only this most recently described Brazilian endemic, but also the many plant and animal endemics (many as yet undescribed) that exist in this extremely diverse area.

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COLOR PLATE

The frontispiece painting by John W. Fitzpatrick has been made possible by an endowment established by George Miksch Sutton.

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HABITAT ASSOCIATIONS OF PIPING PLOVERS WINTERING IN THE UNITED STATES

JANICE L. NICHOLLS AND GUY A. BALDASSARRE[1]

ABSTRACT.—During winter distribution surveys of Piping Plovers (*Charadrius melodus*) on the Atlantic Coast (1986–1987) and Gulf Coast (1987–1988) of the United States we examined factors affecting habitat use and documented associations with other species of shorebirds. Stepwise and discriminant analyses generated models that correctly classified Piping Plover presence 75% of the time for the Atlantic Coast and 65% of the time along the Gulf Coast. The presence of large inlets and passes and mudflats on the Atlantic Coast and beach width, number of small inlets, and beach area on the Gulf Coast appeared as important habitat features affecting presence of Piping Plovers. Both models suggest that habitat heterogeneity (including key feeding sites) may be more important than specific habitat features in affecting winter use of a site by Piping Plovers, however, models only explained 22–28% of the variability in habitat use. *Received 24 July 1989, accepted 10 Feb. 1990.*

The Piping Plover (*Charadrius melodus*) is endemic to North America where recent research has concentrated on breeding biology (Cairns 1982, Burger 1987, Haig and Oring 1988). Piping Plovers spend most of their annual cycle associated with wintering areas (Haig and Oring 1985), yet information on the wintering ecology of this species is sparse. This is significant because Baker and Baker (1973) speculated that winter may be an important portion of the annual cycle affecting mortality of migratory shorebirds. Most investigations of Piping Plovers during winter have occurred recently, and focus on population trends (unpubl. data, C. Raithel, Rhode Island Department of Environmental Management), distribution (Haig and Oring 1985, Nicholls and Baldassarre 1990) and ecology (Johnson and Baldassarre 1988). Few data exist relative to factors affecting winter habitat use.

During Atlantic and Gulf Coast distribution surveys, Haig and Oring (1985) speculated on potential winter habitat preference of Piping Plovers, whereas Johnson and Baldassarre (1988) noted that Piping Plovers wintering in Alabama used sandflats and mudflats versus beaches. However, neither study directly assessed winter habitat use over the broad winter range occupied by Piping Plovers. We studied the winter distribution of Piping Plovers along the Atlantic and Gulf coasts of the United States

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from 1986–1988 (Nicholls and Baldassarre 1990), during which time we quantified habitat characteristics associated with Piping Plovers during winter, and recorded associations with other wintering shorebirds.

STUDY AREA AND METHODS

The methodology associated with the winter distribution survey of Piping Plovers along the Atlantic Coast in 1986–1987 and along the Gulf Coast in 1987–1988 is detailed in Nicholls (1989) and Nicholls and Baldassarre (1990). Sites were surveyed for plovers by walking, or driving a truck or three-wheel all-terrain vehicle. Selected habitat features then were recorded within one-km sections using observed bird(s) as the center point of each section; a new section was sampled if the next bird observed was located outside of the first one-km section. Habitat data also were collected at regularly spaced intervals from sites without plovers. Specifically, all sites ≤three km were sampled as one section, sites 3.0 to 16 km long were sampled once (one-km section) every 1.6 km, sites 16 to 32 km were sampled every four km, and sites >32 km were sampled every eight km. We did not randomly sample non-plover sites because our primary objective was to locate wintering Piping Plovers, thus logistical constraints dictated that we sample sites in sequence. Also, although tidal activity can influence foraging activity of wintering Piping Plovers (Johnson and Baldassarre 1988), we did not control our sampling for tidal effects because we were only interested in presence or absence of Piping Plovers within a sample site rather than a specific behavior.

Habitat variables recorded within each one-km section (from water's edge to vegetation) were visual estimations of the percentages of beach, sandflat, mudflat, dredge spoil, water, and slope of the beach from the water's edge to vegetation (approximated with an Abney level). We also measured the beach width from the water's edge to vegetation, the number of tidepools, the number of ephemeral, small inlets (those not present at low tide), the number of permanent inlets or tidal creeks (medium-sized inlets), and the number of large inlets and passes. We collected substrate samples on the Gulf Coast from each sample section with Piping Plovers and at every fifth non-plover site. Surface and core samples were taken at depths of 0.5 and 5.0 cm, respectively, and analyzed for percent organic matter and percent sand, silt and clay (Soil Survey Staff 1967). For each Piping Plover sighted we also recorded the species and distance to its nearest neighbor as well as the specific microhabitat where each plover was observed (Table 1).

Discriminant function analysis (DFA) was used to develop models that best separated sites (occupied versus unoccupied) based on a subset of the habitat variables measured, and assuming equal prior probabilities (Pimental 1979). Stepwise DFA was conducted to evaluate the importance of individual variables and to eliminate unimportant variables from the model (SAS Institute 1988). Variables recorded as percents were arcsine transformed to meet statistical assumptions of normal distribution. Pearson product moment correlations were calculated between habitat variables and numbers of Piping Plovers. Multivariate analysis of variance (MANOVA) was conducted to test if group means of sites occupied by Piping Plovers differed from unoccupied sites (Pimental 1979).

We recognized two potential problems in the data relative to DFA, which were unequal group sizes, and violation of homoscedasticity. Specifically, the proportion of sites with plovers was smaller (0.25) than the proportion of sample sites without plovers (0.75). However, equal sample sizes created by taking a random sample of the non-plover sites did not improve the DFA results. Plover sites also represented the more homogeneous group (i.e., lower variance) than the non-plover sites, which created unequal dispersions (homogeneity tests were rejected, $P < 0.05$). These violations may affect significance tests associated with

TABLE 1

DESCRIPTIONS OF ATLANTIC AND GULF COAST MICROHABITATS USED BY WINTERING PIPING PLOVERS, DEC. 1986–MAR. 1988

Microhabitat	Description
Mudflat	Dark coloration, *Spartina* sp. nearest veg., soft to walk on, intertidal area generally on the bay side of barrier islands. Substrate characteristics: sand (79.6%), silt (2.2%), clay (2.3%), organic matter (OM) (0.9%); N = 22 sites.
Sandflat	Light brown coloration, dune grasses nearest veg., firm, intertidal area near large inlets/passes or tidepools/dune ponds. Substrate characteristics: sand (96.7%), silt (1.4%), clay (1.0%), OM (0.4%); N = 18 sites.
Sandy mudflat	Orange brown coloration, nearest veg. either dune grasses or *Spartina* sp., firm, intertidal area at overwash sites or inlets with an accreting spit. Substrate characteristics: sand (93.7%), silt (2.0%), clay (1.1%), OM (0.2%); N = 24 sites.
Upper beach	Light coloration, dune grasses nearest veg., soft, non-intertidal area, dry sand area above the berm crest on ocean side of barrier beach. Substrate characteristics: sand (98.6%), silt (1.4%), clay (2.6%), OM (0.6%); N = 6 sites.
Lower beach	Light coloration, dune grasses nearest veg., soft, intertidal area, wet sand or surf zone below the berm crest on ocean side of barrier beach. Substrate characteristics: sand (97.4%), silt (1.3%), clay (1.5%), OM (0.2%); N = 16 sites.
Dredge spoil	Dark coloration, no veg. usually present, soft and uneven surface, man-made areas along the intercoastal waterway. Substrate characteristics: sand (78.9%), silt (3.3%), clay (10.6%), OM (0.5%); N = 3 sites.

DFA (Williams 1981), thus our interpretation was based on the classification procedures and not on significance tests. In other words, we used DFA in a descriptive context rather than a predictive context because we were interested in identifying the variables important in group separation (i.e., plover versus non-plover sites). However, classification functions that predict presence reflect ability to separate groups based on habitat and thus can contribute biologically meaningful information (Green 1971, Rice et. al. 1983, Reinert 1984).

We used *t*-tests to compare habitat and substrate variables at sites occupied vs unoccupied by plovers, and sites with <five individuals (low density) vs >five individuals (high density). We assigned these high and low density groupings after comparing group size frequencies along both coasts (Nicholls 1989). Non-normal percentage data were transformed before all analyses (Zar 1974).

RESULTS

Habitat associations.—Stepwise DFA using the Atlantic Coast data selected the number of large inlets and passes, number of tidepools, % mudflat, beach width, and % sandflat as the major factors affecting plover presence or absence; the model explained 28% of the total variability in

TABLE 2

CORRECT CLASSIFICATION RESULTS OF PIPING PLOVER WINTER HABITAT USING DISCRIMINANT FUNCTION MODELS, DEC. 1986–MAR. 1988

	Percent correct predictions				
Class	Atlantic N = 466	Gulf N = 509	Both coasts N = 975	Atlantic test data[a] N = 233	Gulf test data[b] N = 255
Present	75 (50/67)[c]	65 (83/128)	59 (114/195)	55 (35/50)	63 (50/80)
Absent	84 (334/399)	78 (296/381)	77 (604/780)	70 (150/183)	74 (129/175)

[a] Results of cross-validation test of the Atlantic Coast data.
[b] Results of cross-validation test of the Gulf Coast data.
[c] Number of correct predictions/total number of observations.

habitat use. The Atlantic Coast model correctly classified Piping Plover presence 75% of the time and absence 84% of the time (Table 2). Structure coefficients, which indicate variables most closely associated with the derived function, were 0.686 for the number of large inlets and passes, 0.503 for % mudflat and 0.407 for the number of tidepools, 0.387 for beach width, and 0.341 for % sandflat. The Gulf Coast data then were used to cross-validate the Atlantic Coast function, which correctly identified plover sites 54% of the time and nonplover sites 70% of the time.

Stepwise DFA for the Gulf Coast selected beach width, % beach, % mudflat, and number of small inlets for the presence and absence criterion, and explained 22% of the total variability in habitat use. The Gulf Coast model correctly predicted presence 65% of the time and absence 78% of the time (Table 2). The structure coefficients identified beach width (−0.695), number of small inlets (−0.409), % mudflat (−0.222), and % beach (0.632), as most closely associated with the overall model. Cross-validation was performed by splitting the data and using half to develop a model and the other half to test it; results generally supported the first models. A final DFA was conducted on data combined from both coasts, and correctly predicted plover presence 59% of the time, and absence 77% of the time.

The MANOVA revealed that occupied versus unoccupied sites represented different habitats (Atlantic Coast: Wilk's lambda = 0.66, $F = 18.8$, $P < 0.01$; Gulf Coast: Wilk's lambda = 0.77, $F = 12.3$, $P < 0.01$). The habitat variables % sandflat, % mudflat, the number of medium-sized inlets, and the number of large inlets and passes were different between the Atlantic and Gulf Coast (t-test, $P < 0.05$, Table 2). Combining data from both coasts, the variables % dredge spoil, and number of medium-

TABLE 3

CHARACTERISTICS OF PIPING PLOVER WINTER HABITAT (MEAN ± SE) ON THE ATLANTIC AND GULF COASTS, DEC. 1986–MAR. 1988

Variable	Atlantic Coast			Gulf Coast		
	Present N = 67	Absent N = 399	*P*-value	Present N = 128	Absent N = 381	*P*-value
Beach width (m)	69.3 ± 7.0	45.2 ± 1.8	0.00	74.4 ± 4.7	42.4 ± 2.4	0.00
Slope (%)	0.6 ± 0.2	1.8 ± 0.1	0.00	1.2 ± 0.1	1.9 ± 0.1	0.00
% beach	42.3 ± 4.1	71.1 ± 1.4	0.00	46.1 ± 3.0	71.6 ± 1.8	0.00
% sandflat	31.7 ± 3.6	19.9 ± 1.0	0.00	18.9 ± 2.0	9.1 ± 0.5	0.00
% mudflat	12.9 ± 3.1	2.3 ± 0.6	0.00	21.5 ± 3.0	14.5 ± 1.6	0.02
% water	13.1 ± 1.8	4.5 ± 0.6	0.01	10.3 ± 1.1	4.6 ± 0.5	0.01
No. tidepools	0.7 ± 0.2	0.1 ± 0.0	0.00	0.3 ± 0.1	0.1 ± 0.0	0.01
No. small inlets	0.2 ± 0.0	0.2 ± 0.0	0.63	0.2 ± 0.0	0.1 ± 0.0	0.00
No. medium[a] sized inlets	0.1 ± 0.0	0.0 ± 0.0	0.16	0.1 ± 0.0	0.0 ± 0.0	0.11
No. large[a] inlets/passes	0.5 ± 0.1	0.1 ± 0.0	0.00	0.2 ± 0.0	0.2 ± 0.0	0.01

[a] Represents the percentage of present vs absent cases.

sized inlets did not differ (*t*-test, $P > 0.05$) between sites with or without birds. The variables % dredge spoil, number of small inlets, medium-sized inlets, and tidepools also did not differ ($P > 0.05$) between sites with high (>5) vs low (<5) plovers; all other variables were different ($P < 0.05$). Piping Plovers were observed on sandflats (27%), sandy mudflats (25%), mudflats (21%), upperbeach (14%), lowerbeach (7%), and dredge spoil (6%). The average substrate characteristics further defined these microhabitats (Table 3).

Surface and core substrate data were analyzed separately from habitat data because of the smaller sample size. No differences were found between substrate variables and presence or absence of plovers (*t*-test; $P > 0.05$). No differences ($P > 0.05$) were detected between sites with high and low numbers of plovers except for percent silt, which was greater in the surface sample at higher plover densities.

Interspecific associations and activity.—Piping Plovers almost always were found associated with other species of shorebirds or with other Piping Plovers (Piping Plovers were observed alone <1% of the time). We defined a Piping Plover as alone if no other shorebirds (including another Piping Plover) were within the one-km sample site formed by using the observed Piping Plover as the center point. Eighty-one percent of the Piping Plovers we observed were associated with more than five other shorebird species; only 4% were seen with one to two other species or were seen alone. The

most frequent nearest neighbors were other Piping Plovers (57%), Sanderlings (*Calidris alba*) (11%), Least Sandpipers (*C. minutilla*) or Western Sandpipers (*C. mauri*) (11%), and Semipalmated Plovers (*Charadrius semipalmatus*) (9%). When the nearest neighbor was another Piping Plover, the distance was <1.6 m 50% of the time and 3.3–16.4 m 42% of the time, but <5% for distances >16.4 m, up to 1000 m (0.5 km). Overall, excluding other Piping Plovers as nearest neighbors, plovers were found 44% of the time near species that visually forage (i.e., plovers) and 56% of the time near species that are tactile foragers (i.e., sandpipers).

DISCUSSION

Habitat associations.—The Atlantic Coast test data and the low classification results for the DFA model when both coasts were combined suggest that different habitat variables may affect plover presence depending on the coast. Obvious physical differences exist between the coasts, which may affect shorebird habitat and justify creating separate models. For example, a stepwise DFA analysis using coast as the criterion variable identified percent sand, percent mud, percent beach, and beach width and slope as variables that significantly separated the two coasts.

The combination of habitat variables selected for DFA models on both coasts indicates that environmental heterogeneity may be an important factor differentiating sites that are occupied vs unoccupied by wintering Piping Plovers. For example, although classification results for the coastal models are reasonable, no variable alone was correlated highly with plover numbers or to the models (e.g., Pearson correlation coefficients between each variable and plover numbers were <0.2).

Along the Atlantic Coast the number of large inlets and passes may be an important habitat feature because 72% of sites with Piping Plovers were adjacent to these areas. Sandflats and sandy mudflats often were associated with large inlets and tidepools (also important in the model), and served as foraging areas for other species of wintering shorebirds. The low overall R^2 of 0.28 and a high degree of overlap in discriminant scores also (Nicholls 1989) may imply weak discriminating variables. Nevertheless, DFA did provide a preliminary overview of Piping Plover winter habitat. That the DFA correctly classified nonplover sites better than plover sites may be due to the paucity of birds seen on the Atlantic Coast (i.e., 222 birds; Nicholls 1989, Nicholls and Baldassarre 1990).

Plover sites vs non-plover sites on the Gulf Coast were characterized by greater beach width, greater % mudflats, lower % beach and more small inlets. Our general observations supported these data in that typical plover sites consisted of large areas of intertidal flats. For example, sites with

narrow beaches (i.e., Santa Rosa Island, Florida; Padre Island National Seashore, Texas) often had little shorebird foraging habitat and few Piping Plovers, whereas barrier beaches with overwash areas (i.e., Honeymoon Island State Park, Florida and Chandeleur Islands, Louisiana) or with sections of mudflats (i.e., Rockefeller Refuge, Louisiana) attracted the largest concentrations (Nicholls 1989). The Gulf Coast function also had difficulty separating occupied versus unoccupied sites as reflected in the model R^2 of 0.22. However, the survey accounted for 1508 plovers and 176 wintering sites (Nicholls 1989), which should have contributed to greater group separation.

Misclassification of sites can be explained partially because it was assumed that sites with plovers had suitable habitat, whereas sites without plovers did not necessarily imply unsuitable habitat. Piping Plovers could be "missed" at some sites due to survey timing because Piping Plovers may make local movements within a general area depending on weather and tide conditions (Zivojnovich and Baldassarre 1987, Johnson and Baldassarre 1988). Shorebirds in general often move to alternate feeding habitats due to the cyclic tidal inundation of sand and mudflats (Evans 1976, Burger et al. 1977, Conners et al. 1981). Also, most plovers sighted on this survey were found foraging (72%), which indicates that we had difficulty locating roosting birds. Thus, this study is biased towards sites that had birds at the time of the survey. Additionally, "plover sites" may not be occupied because of the species' rarity. However, our large sample size on both coasts (Table 2) should have helped to ameliorate effects of misclassification.

Although it is difficult to determine habitat preference without exact detail on the availability of each microhabitat, Piping Plovers were observed foraging most frequently on sandflats and sandy mudflats. Further, most invertebrates identified in the fecal samples collected from Piping Plovers (Nicholls 1989, R. Heard pers. comm.) are associated with a wet sand, intertidal area, and sites with high plover densities also had more silt in the surface layer than sites with lower densities. Johnson and Baldassarre (1988) reported that foraging plovers predominantly used protected mudflats or exposed sandflats in Alabama, and Chapman (1984) found that feeding activities of Piping Plovers were confined to moist-sand substrates on Padre Island National Seashore, Texas. Burger et al. (1977) also noted that breeding Piping Plovers preferred the wet sand zone on inner and outer beaches in the Brigantine National Wildlife Refuge in New Jersey. Thus, because Piping Plovers spend a high amount of time foraging during winter (Johnson and Baldassarre 1988) we speculate that sandflats and sandy mudflats may attract the largest concen-

trations of Piping Plovers because of a preferred prey base, and/or because the substrate coloration provides protection from aerial predators due to chromatic matching (Graul 1973).

Interspecific associations.—Piping Plovers usually were found in mixed flocks of shorebirds, which may offer protection from predation (Goss-Custard 1970, Page and Whitacre 1975), or reflect availability of feeding sites (Myers et al. 1979). Piping Plovers appeared to stay together within these groups, however, as the nearest neighbor was another Piping Plover 57% of the time. The other small plovers (i.e., Snowy [*Charadrius alexandrinus*] and Semipalmated) were nearest neighbors only 3.8% and 9.0% of the time, respectively.

Johnson (1987) found that interspecific interactions often involved Snowy (29.4%) and Semipalmated plovers (23.5%). Baker and Baker (1973), however, suggested that individuals with similar foraging behavior should utilize different substrate patches. During this study, Snowy Plovers were observed primarily on the upper beach (37%), whereas Semipalmated Plovers were found mostly on mudflats (46%).

Overall, the habitat variables that may be important to wintering Piping Plovers include large inlets (or passes) and a high percentage of sandflat or mudflat, but the percentage of variability explained by the models is low. However, the identification of specific features responsible for a species' presence can be perplexing, especially if total community structure is the important component (Anderson 1981). Indeed, our data may indicate that distribution of Piping Plovers is correlated more with habitat heterogeneity versus specific habitat features. For example, sites with large concentrations of plovers (i.e., Little Dauphin Island in Mobile Bay, Alabama, and the Laguna Madre, Texas) consist of complex systems with several habitat types (i.e., roosting and feeding) in relatively close juxtaposition. We also believe that within these habitat complexes wintering Piping Plovers may depend on key feeding areas (i.e., intertidal flats) within which they may prefer specific microhabitats. We do not consider the information gained during this study as definitive, however, and do not recommend its use to determine critical wintering habitat. Nevertheless, these data do provide a foundation for future research on the winter ecology of this species.

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SCIENTIFIC SUMMIT ON THE RED-COCKADED WOODPECKER: SUMMARY REPORT

On March 28–30, 1990, the National Wildlife Federation convened a summit meeting of 24 experts on the biology and management of the endangered Red-cockaded Woodpecker (*Picoides borealis*). The Federation's objective in convening the summit was to establish points of consensus among scientists and managers on biological and management needs for protection and recovery of the species. The summit was mediated by a three-member team from the Southeast Negotiation Network. The summit report details areas of consensus, as well as short- and long-term needs of the species and a series of proposed management initiatives.

For a free copy of the report write: National Wildlife Federation, 1718 Peachtree St., Suite 592, Atlanta, Georgia 30309.

Wilson Bull., 102(4), 1990, pp. 591–604

NEST SUBSTRATE VARIATION BETWEEN NATIVE AND INTRODUCED POPULATIONS OF LAYSAN FINCHES

MARIE P. MORIN[1] AND SHEILA CONANT[2]

ABSTRACT.—On Laysan Island, the endangered, endemic Laysan Finch (*Telespiza cantans*) nests almost exclusively in the native bunchgrass *Eragrostis variabilis*. Experimental nest boxes provided were never used for nesting. Marine debris was not used as nest substrate on Laysan Island. In contrast, the introduced Laysan Finch populations on four islands at Pearl and Hermes Reef used a wide variety of native and alien plants as nest substrates, as well as various kinds of human-made debris. However, nest boxes provided at Pearl and Hermes Reef were not used as nest substrates by finches. *Eragrostis variabilis* is uncommon on Pearl and Hermes Reef, except on Seal-Kittery Island, but is common on Laysan where it is the preferred nest substrate. *Eragrostis* is a dense bunchgrass which probably provides the nest with good protection from sun, rain, wind, disturbance, and predators. On Pearl and Hermes Reef, where *Eragrostis variabilis* is uncommon, other plants that provide dense cover are used as nest substrates, and human-made debris that provides some cover is also utilized. It is unclear why nest boxes were never used as nest substrates at either site. We suggest that the conservation of Laysan Finches on Laysan Island will require the maintenance of a native ecosystem where *Eragrostis variabilis* is a major vegetation component. Otherwise, changes in behavior, morphology, and energy expenditure associated with environmental differences are likely to occur, and may have already occurred in the introduced populations on Pearl and Hermes Reef. *Received 13 Nov. 1989, accepted 23 Mar. 1990.*

The endangered Laysan Finch (*Telespiza cantans,* Wilson 1890) is a little known Hawaiian honeycreeper (Fringillidae: Drepanidinae). It is considered an endangered species due to its small natural distribution and its extreme vulnerability to predators and disease (USFWS 1984, van Riper and van Riper 1985:331, Throp 1970). Laysan Finches are known from the islands of Oahu and Molokai as fossils (Olson and James 1982). Historically, Laysan Finches are known to occur naturally only on Laysan Island (Fig. 1), although a small population now also occurs on four of the islands at Pearl and Hermes Reef (PHR; Fig. 2) to which finches were introduced in 1967 (Amerson et al. 1974). At both of these sites, Laysan Finches are the only passerine birds present, although seabirds are numerous and shorebirds are seasonally common. Laysan and PHR are uninhabited except for periodic visits by research biologists. The islands are part of the Hawaiian Islands National Wildlife Refuge which is administered by the U.S. Fish and Wildlife Service.

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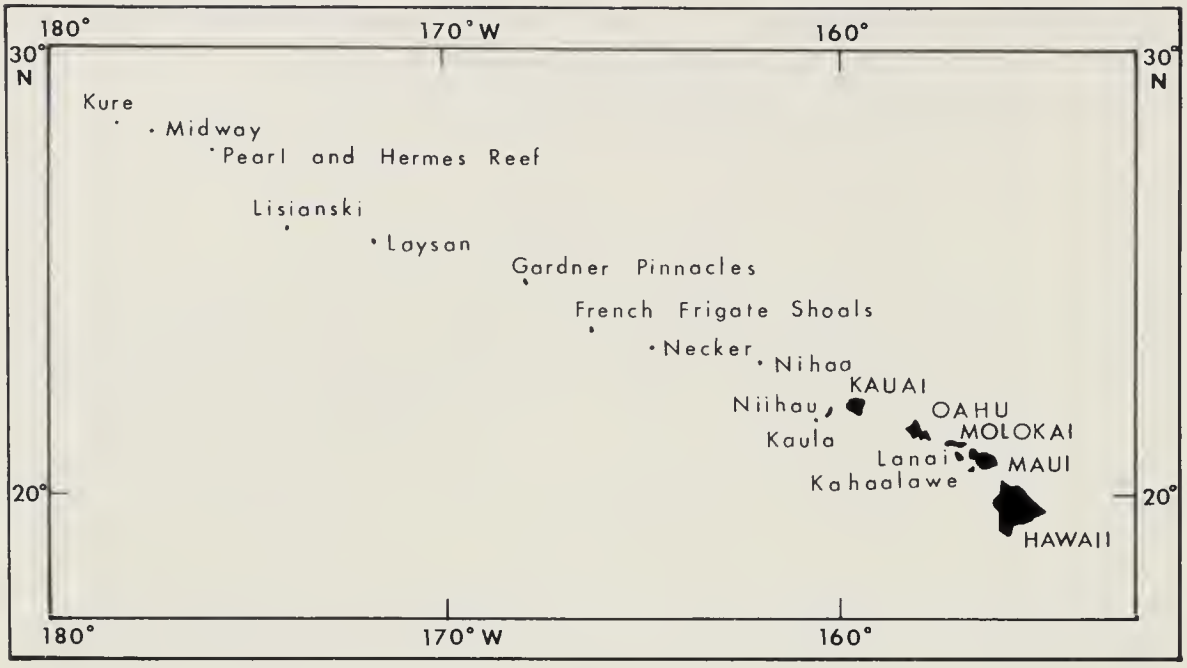

FIG. 1. Map of the Hawaiian archipelago showing the locations of Laysan Island and Pearl and Hermes Reef.

Laysan has a total area of about 397 ha, of which 187 ha are vegetated. This island supports approximately 10,000 Laysan Finches (see Table 1 in U.S. Fish and Wildlife Service 1984). The four main vegetated islands in PHR total 56.2 ha in area, of which 21.3 ha are vegetated (Conant 1988). The current population from this 1967 introduction numbers about 800 birds (Table 1).

Conant has researched the Laysan Finch on Laysan and PHR since 1984, and Morin studied the Laysan Island population from 1986 through 1988. Our work has included records of Laysan Finch nest-site substrates;

TABLE 1

ISLAND SIZE, SUITABLE HABITAT AREA AND LAYSAN FINCH POPULATION SIZE[a]

	Total area (ha)	Vegetated area (ha)	Estimated finch population
Laysan	397	187	10,000
Pearl and Hermes Reef	56.2 (total)	21.3 (total)	820 (total)
Southeast Island	13.8	12.5	520
North Island	6.4	4.4	200
Grass Island	4.4	2.2	50
Seal-Kittery Island	31.6	2.2	50

[a] U.S. Fish and Wildlife Service (1984).

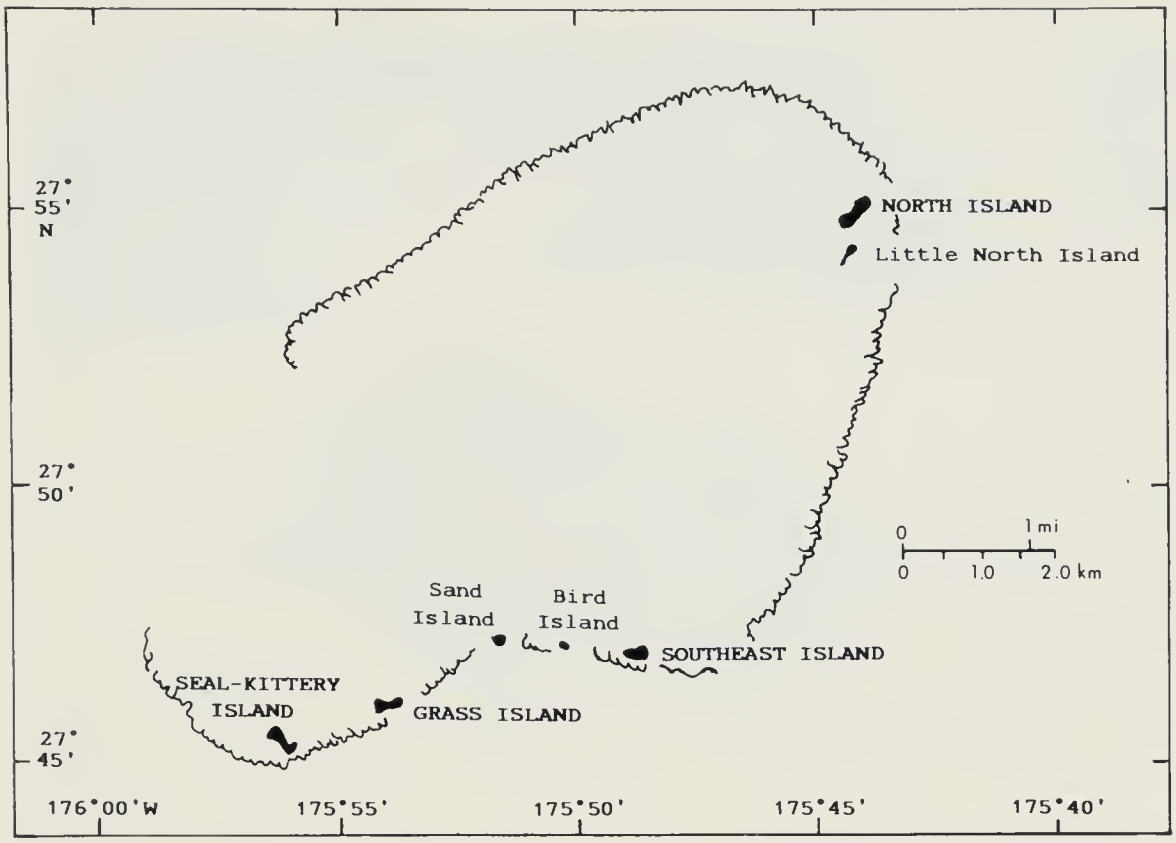

FIG. 2. Map of Pearl and Hermes Reef. Names of islands with Laysan Finch populations are printed in capital letters.

we have also gathered anecdotal information from other researchers (L. Hiruki, B. Choy, C. Rowland and K. McDermond, unpubl. data). Using those data we document in this paper differences in nest-site selection on Laysan versus PHR. The differences appear to be at least partly due to the presence or absence of certain nest substrates.

MATERIALS AND METHODS

In 1986, 62 nest boxes were erected in the northwest quadrant of Laysan Island in an attempt to facilitate the location and monitoring of finch nests. Fifty of the nest boxes were made of plywood, and the remainder were plastic or aluminum elbow pipes and concrete cinder blocks. The nest boxes were randomly located, half of them within *Eragrostis variabilis* clumps, and all but the cinder blocks were approximately 0.3 m above the ground anchored to a stake. Nest boxes were at least 4.5 m from each other, and all were placed in the *Eragrostis* vegetation association (Lamoureux 1963, Newman 1988). The boxes were taken down at the end of the 1986 field season on Laysan. In 1987 20 were reerected on Laysan, and 20 were erected on Pearl and Hermes Reef, where they were placed directly on the ground in the sparse vegetation. All nest boxes were removed from Laysan at the end of the field season in 1988, and most of the boxes at Pearl and Hermes Reef had disintegrated by August of 1989.

Natural nest sites were located on PHR from 1984 to 1989 by Conant and on Laysan

FIG. 3. A clump of the bunchgrass *Eragrostis variabilis* on Laysan Island. When it was photographed, this clump contained an active Laysan Finch nest.

from 1986 to 1988 by Morin. These were discovered using a variety of cues, including male song, female and nestling begging calls, courtship feeding, and by following females with nesting material. Unless otherwise noted, only nests which contained eggs and/or chicks are included in the results section.

During a one-day visit to PHR in 1983 Conant (on Southeast and North Islands) and Gagne (on Grass and Seal-Kittery islands) estimated the number of *Eragrostis* clumps on the four vegetated PHR islands. In July 1989, Conant counted *Eragrostis* clumps on each of the four PHR islands with finches. On Laysan, she counted *Eragrostis* clumps in 30 10 m × 10 m quadrats, with quadrats in the two major vegetation associations where the bunchgrass occurs: 10 in the viney association (*Ipomoea-Boerhavia-Sicyos-Eragrostis*) and 20 in the pure bunchgrass (*Eragrostis*) association. On both Laysan and PHR, Conant noted that she did not count the small (under about 15 cm in diameter) clumps. All plant names used in this paper follow Wagner et al. (1990).

RESULTS

Not a single wooden, pipe, or cement nest box was used as a nest substrate on Laysan in 1986, 1987, or 1988, although in 1987 a finch made a natural nest in the bunchgrass (*Eragrostis variabilis*) 31 cm in front of a wooden nest box in the same bunchgrass clump. The 20 wooden nest boxes placed on PHR in 1987 were erected too late in that breeding season to be used that year. Half of the PHR nest boxes were checked by other researchers in 1988 and all were checked by Conant in 1989, but

TABLE 2
LAYSAN FINCH NEST SUBSTRATES ON LAYSAN ISLAND AND PEARL AND HERMES REEF

	Setaria	*Solanum*	*Tribulus*	*Erag*	*Erag*[a]	Other	Debris[b]
Laysan	0	0	0	199	69	2	0
Pearl and Hermes Reef							
Southeast Island	38	1	0	0	0	7	8
North Island	0	5	4	1	0	5	0
Grass Island	0	1	0	0	0	1	0
Seal-Kittery Island	1	0	0	0	1	1	0
PHR totals	39	7	4	1	1	14	8.

[a] *Eragrostis* with one or more other plant species on or mixed in the clump.
[b] The "debris" category includes such items as plastic crates, "Sono-Buoy" tubes, fishing gear, bamboo poles, a plastic bucket, pipes, hard hats, a TV set, old fuel containers, a generator, swim fins, and a wetsuit.

none had been used. On both Laysan and Pearl and Hermes, Laysan Finches and a variety of seabirds were observed loafing or roosting on or in the shade of the boxes.

Over 270 nests with eggs or chicks were located in natural substrates on Laysan from 1986 to 1988. Of those nests, 73.7% were in *Eragrostis* alone, and 25.5% were in *Eragrostis* with one or more other plant species in or on the bunchgrass clump; only two (<1.0%) of the nests were situated on other substrates. Over 99% were situated in *Eragrostis* (Fig. 3) or were in *Eragrostis* mixed with one or more other plant species (Table 2). When other species were part of the substrate, *Eragrostis* was nearly always the dominant plant, usually with a vine of some sort (most commonly the morning glory *Ipomoea pes-caprae* and/or the native cucumber *Sicyos maximowiczii*) growing over the bunchgrass clump. Only two Laysan nests did not have *Eragrostis* as some or all of the substrate; one was a nest found on the ground under the sedge *Cyperus laevigatus* and the other was a nest built on very low branches of a dead *Pluchea indica* bush heavily overgrown with the succulent ground cover *Sesuvium portulacastrum.*

On PHR the grass *Setaria verticillata* was the most common (38 out of 46) natural nest substrate recorded on Southeast Island. The perennial shrub *Solanum nelsonii* (five out of 12) and the annual herb *Tribulus cistoides* were the most common nest sites on North Island (see Table 2). Other plant species, including *Lepturus repens, Lepidium bidentatum, Boerhavia repens,* and various combinations were used as well. There were several nests built under both active and abandoned Great Frigatebird (*Fregata minor*) nests (particularly in 1989), and a single nest found

TABLE 3

LIST OF PLANT SPECIES ON LAYSAN ISLAND AND THE FOUR VEGETATED ISLANDS OF PEARL AND HERMES REEF[a]

Plant species (status) (alphabetical order)	Laysan	Southeast	North	Grass	Seal-Kittery
Boerhavia repens (I[b])	+	+	+	+	+
Brassica campestris (A)		+			
Casuarina equisetifolia (A)	+				
Cenchrus echinatus (A)	+				
Chenopodium oahuense (H)	+				
Cocos nucifera (A)	+				
Conyza bonariensis (A)	+				
Coronopus didymus (A)		+			
Cynodon dactylon (A)	+	+			
Cyperus laevigatus (I)	+				
Eragrostis paupera (I)		+	+[f]		
E. variabilis (H[c])	+	+	+	+	+
Fimbristylis cymosa subsp. *spathacea* (I)	+				
F. cymosa subsp. *umbello-capitata* (I)	+				
Heliotropium currasavicum (I)	+				
Ipomoea indica (I)	+				
I. pes-caprae subsp. *brasiliensis* (I)	+				
Lepidium bidentatum var. *o-waihiense* (H)		+	+	+	+
Lepturus repens (I)	+	+	+	+	+
Malvastrum coromandelianum (A)		+			
Mariscus pennatiformis subsp. *bryanii* (L[e])	+				
Nama sandwicensis (H)	+				
Nicotiana tabacum (A)	+				
Pluchea indica (A)	+				
Portulaca lutea (I)	+	+			
P. oleracea (A[d])	+	+[f]	+[f]		
Scaevola sericea	+				
Sesuvium portulacastrum (I)	+	+		+	+
Setaria verticillata (A)		+		+	+[f]
Sicyos maximowiczii (H)	+	+	+	+[f]	+
S. pachycarpus (H)	+				
S. semitonsus (H)	+				
Solanum americanum (A)	+	+			
S. nelsonii (H)		+	+	+	+
Sonchrus oleraceus (A)		+			
Tournefortia argentea (A)	+	+			
Tribulus cistoides (I)	+	+	+	+	+

[a] This list includes all species of plants observed or collected from 1983 through 1989, except that *Portulaca oleracea* and *Eragrostis paupera* were seen but not collected on North Island. Historically, other species were known from the islands.

[b] I = Indigenous to the Hawaiian Islands.

[c] H = Endemic to the Hawaiian Islands.

[d] A = Alien, introduced to the Hawaiian Islands.

[e] L = Endemic to Laysan Island.

[f] New island record (Herbst and Wagner, 1990, this study).

FIG. 4. A two- or three-gallon plastic container for liquids containing an old Laysan Finch nest at Southeast Island, Pearl and Hermes Reef. The side of the container was cracked off and removed so the nest could be photographed. Apparently finches entered the container through its neck or "spout."

in a partially collapsed seabird burrow on North Island. Table 3 is a list (alphabetic) of all plants that were observed or collected on Laysan and the four vegetated islands of PHR from 1983 through 1989 (Newman 1988, Herbst and Wagner, in press, Morin and Conant, unpubl. data). Nearly all plant records are substantiated by voucher specimens collected by Conant and deposited in the Department of Botany at the B. P. Bishop Museum. The list includes some new island records and suggests that at least one species, *Achyranthes splendens* may no longer occur at PHR. It should be noted that *Eragrostis paupera* is a diminutive bunchgrass unsuitable as a nest substrate.

Another major nest substrate used on PHR was marine debris (Fig. 4). Marine debris is a highly heterogeneous assortment of man-made flotsam which washes ashore on these very remote islands; these objects are buoyant and are frequently made of plastic or styrofoam. Common marine debris on both Laysan and PHR includes plastic line or rope; plastic or styrofoam floats; various types of fishing nets; plastic toys, bottles, and cigarette lighters; glass bottles and floats; plastic crates, and laundry baskets (Morin 1987). Marine debris was never used as a nest substrate on Laysan.

TABLE 4

ABUNDANCE OF BUNCHGRASS (*ERAGROSTIS VARIABILIS*) ON LAYSAN ISLAND AND PEARL AND HERMES REEF

	Total vegetation (ha)	Number of *Eragrostis* clumps per island	
		1983	1989
Laysan Island	187	no estimate	349,300 ± 53,660[a]
Pearl and Hermes Reef	21.3	337 to 437 (total)[b]	538+ (total)
Southeast Island	12.5	20	2
North Island	4.4	200 to 300	34
Grass Island	2.2	17	42
Seal-Kittery Island	2.2	100	460+

[a] Based on an estimate from counts of 30 10 × 10 m quadrats.
[b] Based on estimates made by Sheila Conant and Wayne Gagne in 1983.

The 30 quadrats in which *Eragrostis* clumps were counted on Laysan Island averaged 34.9 ± 14.37 clumps per 10 m × 10 m quadrat (Table 4). The average number of clumps in the two vegetation associations sampled was not significantly different at the 0.05 level, so the data were lumped. Conservatively estimating that a minimum of 100 ha of Laysan's 187 vegetated ha are either the pure *Eragrostis* or the *Ipomoea-Boerhavia-Sicyos-Eragrostis* association yields a minimum estimate of 349,300 ± 53,660 clumps of bunchgrass on Laysan. On PHR, Conant's 1989 total *Eragrostis* counts yielded 538+ for the entire atoll. In 1983, estimates made by Conant and Wayne Gagne (Table 4) were only slightly lower than the 1989 counts, but Conant, who has spent two to five weeks at PHR in 1984, 1985, 1986, 1987, and 1989 feels Gagne's 1983 estimates (made during half hour insect collecting visits) of clump numbers were low on Grass and Seal-Kittery islands.

Thirteen man-made nest substrates have been used at PHR (Table 2), although not all of these objects are marine debris: the generator, swim flippers, and wetsuit were brought to PHR by researchers. At least eight of the nests found in debris had eggs or chicks, but the remainder may have had neither. All of the nests in man-made objects were on Southeast Island at PHR.

DISCUSSION

We believe there are four factors that influence nest-site selection in Laysan Finches. The first is weather, which varies from intense heat and dryness to windy, cold rain. The extremes of temperature and humidity undoubtedly pose thermoregulatory challenges to finches, especially to

young chicks incapable of temperature regulation. The second is disturbance; seabirds such as Laysan Albatross (*Diomedea immutabilis*) chicks may stand on plants containing finch nests, and Wedge-tailed Shearwaters (*Puffinus pacificus*) burrow under plants containing nests. Third, nest substrate availability is important; if a preferred plant substrate is uncommon or not present at all, a different substrate will be used, possibly at some cost to the bird, such as increased clutch mortality. Finally, although predation on the finches has rarely been observed, field observations suggest that Great Frigatebirds (*Fregata minor palmerstoni*), Bristle-thighed Curlews (*Numenius tahitiensis*) and Laysan Finches themselves are capable of preying on finch chicks or eggs (Dill and Bryan 1912, Walker 1961, Morin and Conant, unpubl. data).

The closely related, endangered Nihoa Finch (*Telespyza ultima*) has nested in captivity in cement blocks and pipes (Berger 1981), and on Nihoa Island they nest in rock crevices and holes (Sincock and Kridler 1977, Conant, unpubl. data). In the early part of this century, when the vegetation on Laysan was nearly eliminated by introduced rabbits, Laysan Finches nested in the crannies of human-made piles of guano blocks, in a manner reminiscent of their Nihoa relatives, and even in one of the guano mining buildings, which no longer exists (Ely and Clapp 1973).

We propose that substrate availability is an important factor that causes Laysan Finches to use different nest substrates on the two atolls. There were early reports of Laysan Finches nesting in the native bush *Chenopodium oahuense* (Fisher 1903a, Fisher 1903b, Rothschild 1893–1900), but by 1923 the plant had been extirpated by the introduced rabbits, which were themselves extirpated by 1924. However, observations made both before and after the devegetation of Laysan mentioned *Eragrostis variabilis* as the primary nest substrate on Laysan Island (Fisher 1903b, Ely and Clapp 1973, Sincock and Kridler 1977, Amadon 1950, Morin, unpubl. data). Laysan and the four islands at PHR have at least some *Eragrostis variabilis,* but *Solanum nelsonii* and the grass *Setaria verticillata* only occur at PHR (Table 4). *Setaria* was most commonly used on Southeast Island in PHR (Table 2), but on North Island, where *Setaria* does not occur, *Solanum nelsonii* and *Tribulus cistoides* were the most common nest substrates.

To summarize, *Eragrostis* occurs on all the islands, and is the preferred nest substrate on Laysan (Table 2), but it is seldom used on PHR, probably because it is relatively uncommon (Table 3). There are about 10,000 finches on Laysan, and about 800 finches at PHR. The ratio of bunchgrass clumps to finches on the two islands is dramatically different: about 35 clumps per finch on Laysan and <1 clump per finch at PHR. The PHR island with the most Laysan Finches, Southeast Island, has almost no

Eragrostis. This probably accounts for the fact that so many other nest substrates, such as *Setaria* and marine debris, were used there. *Setaria* is an introduced sod-forming (rather than bunch-forming) grass. Although the growth forms of *Setaria* and *Eragrostis* differ, the type of cover they provide for nests is similar. However, *Setaria* is shorter and less dense. North and Seal-Kittery Islands were the only PHR islands where *Eragrostis* was used as a nest substrate, either alone or in combination with other plants.

In the absence of data on the introduced finch population at PHR, one might conclude that Laysan Finches were obligate *Eragrostis* nesters. However, other plants that provide suitable, dense cover are selected as nest substrates when *Eragrostis* is uncommon. Although Laysan Finches are endemic to the hot, treeless atoll environment, their physiological heat tolerance is no better than that of most passerines (Weathers and van Riper III 1982). However, the basal metabolic rate of Laysan Finches is 20 per cent lower than would be predicted for a passerine of this size, indicating some adaptation to the warm environment (Weathers and van Riper III 1982). Because heat tolerance would be important to incubating birds forced to remain in the nest, nest substrate selection may represent a behavioral adaptation to the extremes of heat and insolation.

The presumed nesting requirements of the Laysan Finch (i.e., shelter from sun, rain, wind, and avoidance of predators or other disturbances) appear to be met by the plants or other substrates (e.g., Great Frigatebird nests) that provide the densest cover. It is unclear why finches on Southeast Island will nest in a wide variety of marine debris, but will not use wooden nest boxes. Inadequate size, poor ventilation and the presence of introduced, moisture-loving ants may explain the puzzle.

The fact that marine debris was not used as a nest substrate on Laysan Island suggests that appropriate nest sites are not limited. The frequent use of debris and other man-made objects as nesting sites on Southeast Island can be explained in several ways. First, suitable natural nest sites may be limited at Southeast Island at PHR. Second, relatively more man-made nest substrates are available because researchers (and their attendant gear) spend most of their time on Southeast Island when working at PHR. Third, more marine debris washes ashore on Southeast Island (Amerson et al. 1974), possibly due to its location in the reef (Fig. 2). Finally, the island was used for military exercises during World War II, was the site of unauthorized military operations in the 1950s, and was the site of a pearl oyster fishery in the late 1920s (Amerson et al. 1974). All of these human activities left various kinds of debris on the island.

Regardless of whether finches on Southeast Island prefer marine debris as a nest site or simply use it because suitable natural sites are limiting,

it is clear that our nest box designs appear to be unsuitable nest substrates. Should it be desirable to increase nest substrate availability (at least on Southeast Island), it may be most expeditious to simply increase certain types of marine debris.

The results of this study raise the question, "How do human actions affect adaptation of an introduced species to its new habitat?" Conant (1988a) has documented significant morphological differences in the Laysan and the introduced PHR Laysan Finch populations. Although these two atolls share many plant species, plant community structure is more complex on Laysan than on PHR, particularly at the level of nest substrate for a passerine bird. It seems quite possible that the differences in vegetation may exert selective pressure on finches in a number of ways. One might speculate, for example, that a nest in open and/or sparse vegetation or in a plastic crate may require different parental behaviors and energy expenditures than a nest in dense vegetation.

How Laysan Finches affect the plant species in which they nest is also of concern. In addition to invertebrates, eggs, and carrion, Laysan Finches eat a wide variety of plant species and plant parts, including *Eragrostis* seeds; the birds also destroy grass leaves when they mandibulate the stems. Descriptions of Southeast Island from the early 1920s and 1930s (Amerson et al. 1974) reported *Eragrostis* to be a dominant plant in the community. Wave overwash of this low (<4.5 m) island during a severe storm in 1930 is believed to have caused a major plant die-off. By 1974, *Eragrostis* was considered an insignificant component of the vegetation on Southeast Island (Herbst 1980, Amerson et al. 1974). Estimates in 1983 and counts in 1989 of the number of *Eragrostis* clumps (Table 4) show that at least one of the four islands at PHR experienced a decline of *Eragrostis* between 1983 and 1989.

Laysan Finch breeding was monitored after their introduction to Southeast Island at PHR in 1967. Summarizing data collected up to 1969, Amerson et al. (1974) stated that (on Southeast Island) "Most nests are in *Eragrostis* clumps and a few are in the moderately dense *Solanum.*" Later, Sincock and Kridler (1977) reported that 90% of the Southeast Island nests found from 1967 through 1974 were located in *Eragrostis.*

Finches feed on seeds of *Setaria, Tribulus, Eragrostis, Boerhavia,* and *Sonchrus.* We have observed them eating the seeds of nearly every species of plant at PHR, and Herbst (pers. comm.) found that *Eragrostis* inflorescences he examined on trips in 1981 and 1988 had been nearly stripped of seeds by foraging finches. High water in a severe 1969 storm destroyed the largest *Eragrostis* stand on Southeast, which had not recovered by 1974. How the storm affected the grass on other islands is unknown, although the vegetated portion of Seal-Kittery Island, where *Eragrostis*

is still quite abundant, is two to three meters higher in elevation than any of the other islands at PHR. We believe it is possible that the finches' feeding habits may have prohibited the recovery of *Eragrostis,* and possibly even hastened the decline of *Achyranthes splendens* at PHR. Thus, the vegetation composition at PHR may be effecting a change in the nest-site selection of the finches, while the finches may simultaneously be changing the composition of the vegetation.

Extrinsic factors such as thermal characteristics, substrate availability, protection from predators (especially predation of eggs by other finches) and disturbance, may all affect nest placement. According to Brown and Goertz (1978), Munro and Rounds (1985), and Osborne and Osborne (1980), the characteristics of potential nest substrates, such as height, sturdiness, and density of cover, may be more important than the species of plant used for a nest substrate. However, *Eragrostis* apparently provides the ideal substrate for Laysan Finch nests: insulation for nests from the sun and rain and protection from predators and other forms of disturbance. In addition, finches roost in *Eragrostis* clumps, eat its seeds and glean invertebrates from its foliage. Some shrubs (e.g., *Pluchea indica, Scaevola sericea, Tournefortia argentea*), and a small number of trees (one *Casuarina equisetifolia* and about thirty *Cocos nucifera*) occur on Laysan, but Finches have not used these as nest sites.

We have found that the nest substrates used by an introduced population may be unexpectedly different from those of the parent population if habitat composition and structure differ. Whether or not these differences have influenced divergence of the Laysan and PHR Laysan Finch populations is unknown. How the introduced finches have affected the plants and invertebrates at Pearl and Hermes Reef is also unknown. We believe that the conservation of the endangered Laysan Finch will require the maintenance of an unaltered ecosystem on Laysan where *Eragrostis* is maintained as a major vegetation component that provides food, roosting, and especially nesting sites for Laysan Finches.

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SIGURD T. OLSON COMMON LOON RESEARCH AWARD

LoonWatch is accepting applications for its sixth annual award for research on Common Loons in the Western Upper Great Lakes region of the United States and Canada. To apply for cash awards up to $2000, a brief description (maximum 10 pp.) of the proposed research program and curriculum vitae should be submitted by the principal investigator to Terry Daulton Dunn, Coordinator, LoonWatch, Sigurd Olson Environmental Institute, Northland College, Ashland, Wisconsin 54806. Proposals must be received by January 10, 1991. Proposals by students should be accompanied by two letters of recommendation. The award will be granted on the basis of the project's potential to better understand and manage Upper Great Lakes populations of Common Loons. Guidelines for applicants are available from LoonWatch.

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BREEDING BEHAVIOR OF AMERICAN KESTRELS RAISING MANIPULATED BROOD SIZES IN YEARS OF VARYING PREY ABUNDANCE

NICHOLAS W. GARD AND DAVID M. BIRD[1]

ABSTRACT.—Behavioral responses of American Kestrels (*Falco sparverius*) to manipulated broods of two, five, and seven young were studied in southwestern Quebec during 1986 and 1987. Average territory size was inversely correlated with small mammal abundance which differed significantly between years, but was not influenced by brood size in either year. Parents of all three brood sizes devoted less time to searching for food, and more time to resting and maintenance behavior in 1987 than 1986. Interannual differences in hunting behavior were attributable to variations in the percent time spent perch-hunting. Hover-hunting times were similar between years and among brood sizes. Despite less time spent hunting, rates of prey capture and food delivery to the nest were significantly higher in 1987.
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According to Lack's (1954, 1968) hypothesis, the observed average brood size should produce the greatest number of young surviving to fledging. Studies in which brood size has been experimentally enlarged have more often than not refuted Lack's theory by finding the most productive brood size to be larger than the average brood size (Martin 1987). Reproductive success in one breeding season represents only a portion of the total lifetime output for an iteroparous species. Increasing reproductive success at any one breeding attempt may require a greater expenditure of reproductive effort by the parents resulting in a decreased probability of survival to the next breeding attempt. Therefore, individuals may raise broods smaller than the most productive size to maximize lifetime reproductive output (Williams 1966, Charnov and Krebs 1974).

Differential parental mortality in relation to brood size is difficult to detect since low recovery rates of banded individuals necessitate large sample sizes to demonstrate the existence of significant differences (DeSteven 1980, Nur 1984a). Monitoring parental weight changes during the breeding season can provide an indirect measure of the cost of reproduction, although the relationship of parental weight loss to post-reproductive survival is unclear (Martin 1987, but see Nur 1984a). Furthermore, weight loss during breeding has been suggested to be an adaptation which lessens the energetic expenditure associated with heightened feeding activity (Freed 1981, Norberg 1981).

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Reproductive effort can also be estimated indirectly by observing parental behavior and rates of food provisioning to the young in relation to variation in brood size. Subsequent adult survival cannot be ascertained by this procedure, but it can indicate whether parents respond to changes in brood size by modifying foraging costs, or whether they are near the limit of their reproductive capabilities as Lack (1954, 1968) suggested. We report here on the influence of experimental manipulation of brood size on parental behavior and feeding frequency in the American Kestrel (*Falco sparverius*).

METHODS

This study was performed from April to July 1986 and 1987 in southwestern Quebec. We used a population of wild kestrels breeding in nestboxes erected by the Macdonald Raptor Research Centre in the western region of the island of Montreal, Ile Perrot and eastern Vaudreuil-Soulanges County. Nestboxes were placed on hardwood trees or snags located in hedgerows bordering abandoned agricultural fields.

Breeding records for the wild population for the four previous years indicated that broods of five produced, on average, the greatest number of young surviving to fledging (unpubl. data). We manipulated broods of five to create small and large broods of two and seven young, respectively. Manipulations were always performed within two days of the hatching of the last young. To minimize age and weight differences, we only transferred chicks between nests in which young had hatched within one day of each other.

Parental behavior was recorded during 2-h observation periods. Observations were taken from partially concealed positions about 50–100 m from the nestboxes, and were performed throughout the nestling period. Observation sessions were early morning (07:00–11:00 EST) and late afternoon (15:00–17:30), as birds were usually inactive around midday (pers. obs.). To eliminate bias due to pre-fledging mortality, we only observed nests where all the young were present. Data from all nests of equivalent original brood size were pooled for statistical analysis. Behavioral observations were recorded using a raptor actigram, an ethogram with alphanumeric notations (Walter 1983). The duration of each behavior was recorded and the behavior was classified into one of five categories: hunting, perched, maintenance, caring for the young, and interspecific behavior. Hunting included periods of flapping or soaring flight interspersed with bouts of hover-hunting. Perch-hunting, where birds were observed continually moving their heads and scanning the surroundings, was also included in this category. The latter was differentiated from perched (or resting) behavior where kestrels perched but were not alertly monitoring their territory. Direct flight between perches was also included with perched behavior. Maintenance activities included feeding, preening, or scratching sessions. Caring for the young (brooding or feeding) could not be observed directly, but was inferred from time parents spent in their nestbox. Percentage time data were transformed with an arcsin square root transformation prior to statistical analysis (Sokal and Rohlf 1981). In conjunction with behavioral observations, we recorded rates of prey capture and the number of food deliveries to the nest. Prey capture rates were determined either directly by viewing kestrels diving into the vegetation and emerging with prey, or indirectly by observing kestrels returning to a perch in possession of prey after having previously flown off without a prey item.

To determine relative prey abundance, snap-trapping for small mammals was performed at active nests. Trapping was done near locations where kestrels were observed hunting, and in similar habitats. At each site, 36 Victor snap traps, baited with peanut butter and

rolled oats, were laid out 5 m apart in a 6 × 6 grid arrangement. Traps were checked each morning for ten consecutive days. At least four times during the nestling period, sweep-net samples were collected near active nests to monitor the abundance of grasshoppers, often a major prey item of American Kestrels (Palmer 1988). However, samples were only assessed qualitatively to determine when peak abundance occurred.

The sizes of breeding territories were determined with a spot-mapping technique. The location of kestrels in relation to geographic landmarks such as buildings, roads, hedgerows, or dead snags was marked on acetate overlays of 1:15,000 scale aerial photographs. To compensate for variations in altitude on the photographs, the exact scale was determined by a photo scale reciprocal formula based on ground distances derived from a 1:20,000 scale topographical map (Avery and Berlin 1985). Using a minimum of 20 mapped points, territories were considered as the maximum polygon area created by connecting the outermost locations to form a convex polygon (Odum and Kuenzler 1955). Area of the territory was measured using a dot-grid technique (Avery and Berlin 1985).

All statistical tests followed procedures from Sokal and Rohlf (1981). Reported values are mean ± one SD.

RESULTS

Kestrels maintained smaller breeding territories in 1987 than in 1986. Parents of all three brood sizes displayed this trend, with differences between years being significant for parents raising broods of two or five young (Table 1). However, within each year there was no significant difference in territory size corresponding with variations in brood size (Kruskal-Wallis test, $P > 0.25$ for both years). In 1987 there was a trend for territories to be larger with increasing brood size. This may have been significant if sample sizes were larger.

Average small mammal abundance, as estimated by snap-trapping, was 3.84 ± 4.03 mammals/100 trap nights in 1986 (N = 10 trap sites), and 38.23 ± 23.15 mammals/100 trap nights in 1987 (N = 7 trap sites). The difference between years was highly significant (Mann-Whitney test, $U = 7$, $P < 0.01$). Meadow voles (*Microtus pennsylvanicus*) constituted the greatest proportion of mammals caught in both years: 68.9% in 1986 (106 mammals total caught), and 97.1% in 1987 (725 mammals total caught). Shrews (*Sorex cinereus* and *Blarina brevicauda*) composed 22.6% of the total in 1986 and 1.9% in 1987. Deer mice (*Peromyscus maniculatus*) formed the remainder in both years. Territory size was negatively correlated with estimates of local small mammal abundance (Spearman's $r = -0.770$, N = 17, $P < 0.005$; Fig. 1).

Although sample sizes are too small to permit intra-annual comparisons of prey density in relation to brood size, the general trend of increased mammal abundance in 1987 likely applies at all breeding territories. In both years of this study, several trapping sites were situated between two neighboring nests with different brood sizes. Qualitatively, vegetative structure in these breeding territories and at the trap site appeared similar,

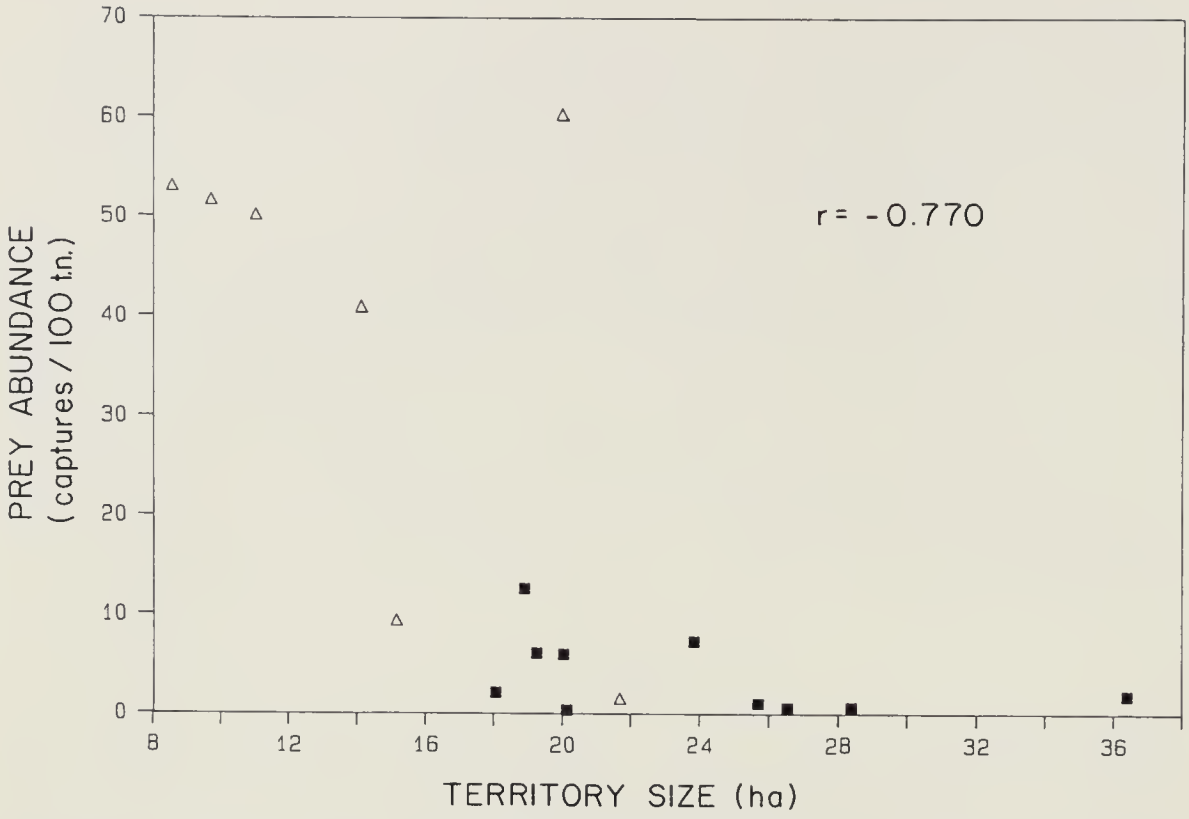

FIG. 1. Territory size of American Kestrels in relation to relative small mammal abundance (captures/100 trap nights). Squares = 1986 territories; triangles = 1987 territories.

so mammal abundance at the trap site probably reflects a reasonable estimate of prey availability at all nearby sites.

Climatic factors were similar during breeding periods in both years. In the region of the study area, total precipitation during the nestling stage in 1986 (1 May to 30 June) was 198.2 mm and average temperature was 14.9°C. In 1987 the nestling stage spanned from 1 May to 6 July, and in that period total precipitation was 192.0 mm and average temperature

TABLE 1

SIZE OF BREEDING TERRITORIES (HECTARES) OF AMERICAN KESTRELS IN 1986 AND 1987 IN RELATION TO BROOD SIZES ESTABLISHED BY EXPERIMENTAL MANIPULATION

Brood size	1986		1987	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
2	7	21.3 ± 4.0	5	11.3 ± 2.1[a]
5	4	27.6 ± 7.6	6	12.4 ± 2.9[b]
7	5	22.5 ± 5.0	4	16.3 ± 5.9
Pooled	16	23.2 ± 5.6	15	13.1 ± 4.0[a]

[a] $P < 0.01$; [b] $P < 0.05$, Mann-Whitney U-test, for differences between years.

TABLE 2

TIME-ACTIVITY BUDGETS FOR AMERICAN KESTRELS REARING VARIOUS SIZED BROODS ESTABLISHED BY EXPERIMENTAL MANIPULATION

Brood size	Sex	Year	Hunting			Perched	Maintenance	Care of young
			Hover	Perch	Total			
2	M	1986	3.3	71.2[b]	74.1[b]	21.0	4.4[b]	0.1
		1987	5.7	42.4	50.1	39.0	12.6	0.1
	F	1986	4.5	44.5[b]	49.0[a]	25.7[a]	3.0	21.7
		1987	3.9	15.5	19.4	53.8	7.6	18.7
5	M	1986	3.4	79.5	82.9	15.0	2.0	0
		1987	3.7	61.8	65.5	29.1	4.8	0.6
	F	1986	4.3	39.2	43.5	38.2	3.2	14.8
		1987	2.1	34.8	36.9	46.0	4.5	12.7
7	M	1986	3.6	78.3[b]	81.9	17.2	0.8[b]	0
		1987	2.8	68.0	70.8	22.8	5.5	0.7
	F	1986	2.2	63.2[a]	65.4[a]	16.7[a]	2.7	14.2
		1987	4.6	27.0	31.6	50.0	2.7	15.3

Values that differ significantly between years for each activity are noted as [a] $P < 0.01$; [b] $P < 0.05$, Mann-Whitney *U*-test.

was 15.8°C (Environment Canada 1986, 1987). Weather has been shown to explain only a minor proportion of variation in small rodent activity (Vickery and Bider 1981), therefore differences in trapping success between years likely reflect actual interseasonal variations in prey abundance and not changes in behavioral patterns produced by environmental conditions.

We observed parent birds for 77.7 h in 1986 and 60.6 h in 1987. Time activity budgets revealed that parents of all brood sizes devoted less time to hunting in 1987 than in 1986 (Table 2). Differences were significant for parents with broods of two, and for females with broods of seven (Mann-Whitney *U*-test, $P < 0.05$). For males rearing broods of seven, the difference approached significance ($P = 0.051$). The percent of total time parents spent hunting from flight was not significantly different between years for any brood size. Therefore, decreases in total hunting time were primarily a result of less time spent perch-hunting. Within each year, the total time spent hunting did not differ significantly among brood sizes for either sex (Kruskal-Wallis test, $P > 0.10$ in all four cases). Although males of all brood sizes spent more time hunting than females, these differences were only significant for broods of two and five in 1986 and broods of seven in 1987 (Mann-Whitney *U*-test, $P < 0.05$ in all three cases). Kestrels responded to decreased hunting time in 1987 by allotting more time to resting or maintenance activities (Table 2). Parents of all

TABLE 3

CAPTURE RATES FOR VERTEBRATE PREY AND DELIVERY RATES TO THE NEST BY AMERICAN KESTRELS RAISING VARIOUS-SIZED BROODS ($\bar{x} \pm$ SD) IN 1986 AND 1987

	Brood size	1986	1987
Prey capture (prey items/h)	2	0.51 ± 0.41	1.37 ± 0.95[b]
	5	0.44 ± 0.73	0.88 ± 1.20
	7	0.26 ± 0.39	0.99 ± 0.80[a]
	Pooled	0.41 ± 0.49	1.03 ± 0.96[a]
Prey delivery (prey items/h)	2	0.33 ± 0.56	0.58 ± 0.47
	5	0.25 ± 0.38	0.45 ± 0.69
	7	0.18 ± 0.29	0.91 ± 0.77[a]
	Pooled	0.26 ± 0.43	0.70 ± 0.70[a]

[a] $P < 0.01$; [b] $P < 0.05$, Mann-Whitney U-test, for differences between years.

brood sizes spent more time involved in these behavioral patterns in 1987 than in 1986. Differences between years were generally not significant, although females raising two and seven young spent significantly more time at rest in 1987 than in 1986 (Mann-Whitney U-test, $P < 0.01$). Females usually spent more time perched than males, but differences were only significant for broods of five in 1986 and broods of seven in 1987 (Mann-Whitney U-test, $P < 0.05$).

For all brood sizes, females spent similar amounts of time brooding and feeding young as inferred from time spent in the nestbox (Table 2). Early in the nestling stage females probably devoted most of their time to brooding young until they were able to maintain effective thermoregulation (Dunn 1979). Later, when young grew too large to brood, time spent in the nestbox probably reflects bouts of feeding. Males spent almost no time in direct care of the young.

Agonistic interactions with other birds, which accounted for less than 0.5% of the total activity budget, have been omitted from the following discussion.

A comparison of all breeding pairs, independent of brood size, revealed that the capture rate for vertebrate prey was over twice as high in 1987 than in 1986 (Table 3). Parents of all brood sizes had greater hunting success in 1987 as compared with 1986, with differences being significant for parents raising broods of two and seven. Within each year however, there was no significant difference in hunting success among brood sizes (Kruskal-Wallis test, $P > 0.15$ in 1986, $P > 0.25$ in 1987).

The proportion of invertebrates to vertebrates in total prey captures was not known, but sweep-net surveys suggested that grasshopper and

cricket abundance during the nestling period was low. Peak invertebrate abundance did not appear to occur until after the young had fledged. Seasonal dietary changes from vertebrate to arthropod prey (Balgooyen 1976, Phelan and Robertson 1978) may have occurred at this time. Insects probably did not constitute a major part of the diet of parents during the nestling period. Parents were not observed delivering insects to the young.

Trends in the rate of vertebrate prey deliveries to young paralleled those observed for prey capture rates (Table 3). Small mammals formed 73.7% of the total vertebrate prey deliveries in 1986 and 78.7% in 1987. These values likely underestimate the true proportion, as it was not always possible to make a positive identification of the prey item delivered. Unidentified prey made up 15.8% of all deliveries in 1986 and 19.1% in 1987; some of these were probably small rodents. Birds and snakes accounted for the remainder of the prey items in both years. For all brood sizes, parents provided young with more prey per hour in 1987 than in 1986, although a significant increase was noted only for broods of seven in 1987 (Table 3). Within each year, the rate of food delivery was not related to brood size (Kruskal-Wallis test, $P > 0.50$ in 1986, $P > 0.10$ in 1987).

DISCUSSION

Territory size of breeding American Kestrels varied inversely with small rodent density. Differences in average territory size between years in response to changes in prey density would appear to support the hypothesis that kestrels are directly monitoring prey abundance and adjusting breeding territory size accordingly. This is supported by a previous study (Bowman and Bird 1986) at the same site that reported a similar inverse relationship between prey abundance and kestrel territory size. Microtine rodent abundance in the earlier study was similar to our estimates for 1986, and territory sizes during these two periods were nearly identical (24 ± 4 ha, Bowman and Bird (1986); 23.2 ± 5.6 ha, this study for 1986). Alternatively, although not examined, territories might have been established based on vegetative structural features correlated with expected prey abundance (Smith and Shugart 1987). The extent of the foraging area did not vary significantly in response to changes in energetic demands associated with differences in brood size. Kestrels may not alter territorial boundaries once established, particularly if the original territory maximizes rates of prey capture while minimizing costs associated with territorial defense. In 1987 birds raising seven young tended to have slightly larger territories compared with other brood sizes, but rates of prey capture were similar. Therefore, an increase in territory size does not appear to improve hunting success.

The significantly lower feeding rates of young by parents in 1986 are probably attributable to reduced prey abundance in that year relative to 1987. Pre-fledging mortality from starvation was high for broods of five and seven in 1986 (Gard 1989), indicating that parents were unable to adequately feed average and enlarged broods.

Prey densities were much higher in 1987 than in 1986. While parents with broods of two and five spent less time hunting in 1987 than in 1986, their rates of prey capture were much higher. Decreased hunting time suggests that because of greater prey abundance and enhanced hunting success in 1987, kestrels could capture sufficient food to meet nestling and adult requirements in a shorter span of time than in 1986. Parents rearing seven young also spent less time hunting in 1987, and had significantly higher prey delivery rates than in 1986. Total time spent hunting by parents with five or seven young was, however, similar in 1987. Parents rearing seven young made more prey deliveries than parents with smaller broods, although the increase was not significant. Several pairs of kestrels were capable of raising all young in a brood of seven to fledging in 1987, but these young fledged significantly lighter than young in broods of five (Gard 1989). This may have resulted in higher post-fledging mortality, as evidence from other studies indicates that post-fledging survival is correlated with fledging weight (see Martin 1987). Variations in prey abundance suggest that kestrels were not always food limited, and that the inability to rear young in enlarged broods to normal fledging weights in 1987 may have been due to adaptive limitations upon parental feeding behavior as proposed by Hussell (1972) and Nur (1984b). As Hussell (1972) noted, other activities (e.g., rest, maintenance) also have a selective value in terms of maximizing lifetime reproductive output. Therefore, amount of food brought to the young may be limited not by the environmental food supply, but by a behavioral component which restricts the amount of time parents spend food gathering irrespective of brood size.

Hover-hunting never accounted for more than 20% of the total time spent hunting, a ratio corresponding with values reported in other studies (Balgooyen 1976, Rudolph 1982, Toland 1987). The proportion of time spent hover-hunting was larger in 1987 than 1986 due to the relatively greater use of perch-hunting in 1986 than in 1987. This is in accord with theoretical models which predict switching to energetically less expensive hunting methods when prey abundance declines (e.g., Norberg 1977). Since the percentage of the total daily activity budget spent hover-hunting does not vary between years or brood sizes, this activity may represent an energetic ceiling on parental performance (Drent and Daan 1980). Hover-hunting has been found to yield higher rates of prey capture and

gross energy intake than perch-hunting. However, energetic consumption during hovering and forward flight is estimated to be about seven times greater than while at rest (Rudolph 1982).

Habitat physiography can be a contributing factor. Toland (1987) noted that kestrels in Missouri favored foraging in mowed or grazed pastures where they hunted primarily from perches. When birds hunted in undisturbed, tall grass meadows a significant increase in hover-hunting was noted, with this strategy comprising 27% of total hunting time. High vegetation in fallow fields made prey detection from perches more difficult. In this habitat, kestrels presumably were compelled to spend more time hover-hunting to maximize prey detection and capture rates despite the higher energetic costs associated with this hunting method. In our study, most territories were in undisturbed fields where vegetational height increased throughout the breeding season. Kestrels may have maximized the time spent hover-hunting in order to capture sufficient prey to meet nutritional demands. The lack of difference in hover-hunting time among brood sizes or years is consistent with the hypothesis that kestrels were at an energetic ceiling for this activity. For parents raising enlarged broods, increasing time engaged in hover-hunting behavior may have incurred physiological costs which outweigh benefits expressed as increased prey capture rates and hence, increased offspring feeding rates (Nur 1984b).

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BREEDING BIOLOGY OF AMERICAN CROWS

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ABSTRACT.—The breeding biology of cooperatively breeding American Crows (*Corvus brachyrhynchos*) was studied on Cape Cod, Massachusetts, from 1983–1987. The study site consisted of habitats ranging from a remote barrier beach to populated suburban areas. Family groups ranged in size from two to 10 members, the latter including an adult pair with their one- to four-year-old offspring. Territories were defended year-round and the mean territory size was 42.1 ha. The mean distance between nests of bordering territories was 0.86 km. Most (88%) nests were built in pitch pine (*Pinus rigida*) trees. Mean nest depth was 24.1 cm, mean total diameter of the nests was 40.7 cm, and the mean diameter of the nest cups was 23.8 cm. Nest height averaged 9.7 m; mean tree height was 10.9 m. Incubation occurred between March and June over an average of 22.3 days. The mean number of days until fledging was 30.1. Reproductive success was measured through the mean number of surviving fledglings. The total mean was 2.0 (N = 46). There was a trend towards increased fledgling production in family groups with six or more members (N = 10, $\bar{x} = 2.6 \pm 1.7$).
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Relatively little is known about the breeding biology of North American *Corvus* with the exception of Northwestern Crows (*Corvus caurinus*) (Butler 1974, Verbeek and Butler 1981, Verbeek 1982, Butler et al. 1984). We report here the demographics and breeding biology of a population of American Crows (*C. brachyrhynchos*) located on Cape Cod, Massachusetts. Accounts that exist on American Crows have described the natural history of populations in other regions of the United States (Good 1952, Graber et al. 1987) and of the Florida race (*C. b. pascuus*) (Kilham 1984a, b, c; 1985a, b; 1986a, b).

STUDY AREA AND METHODS

The study was conducted continuously from 1983 through 1987. The data presented here are part of a long-term study of reproductive success and life history patterns of crows in two disparate habitats. One area, a seven km-long barrier beach (Sandy Neck, Barnstable, Massachusetts), was bounded by a 3200 ha salt marsh to the south and Cape Cod Bay to the north. The barrier beach was characterized by dunes on the north and south and interior patches of maritime forest (approximately 100 ha or 17% of the barrier beach). The barrier beach was subject to seasonal human recreational activities, primarily along the beach front. In contrast, the other study site was located in the developed areas of Barnstable, Massachusetts, which included residential, business, and recreational locations. This area was approximately 150 ha, consisting entirely of broken habitat. Data were collected using binoculars (7 × 35), spotting scopes (30×), and recorded through field notes, 35 mm pho-

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tography, and audio and video recordings. Group sizes were standardized for comparison by determining the number of territorial adults at the onset of incubation. We delineated territories on an U.S. Geological Survey Map (scale 1:24,000) by connecting the locations of displays and fights between neighboring groups. The territory sizes were measured with a planimeter. In areas where there was a tidal flow we measured the territory size during high tide.

Nests were located by following crows carrying sticks and observing nest building or by tracing a unique vocalization made by the incubating female breeder (Kilham 1986b). Nest distances were determined by marking their locations on the U.S. Geological Survey Map and then measuring the distances between them with a ruler. We measured nest dimensions while the nestlings were being banded or at the time of nest failure. Nestlings were banded with U.S. Fish and Wildlife aluminum leg bands and unique combinations of colored, plastic leg bands.

RESULTS

Group sizes.—Crows in our study site usually bred cooperatively (94.4%, N = 54) and the offspring remained within the family units throughout the year. Group sizes ranged from two to 10 members (Table 1). The mean group size was 4.4 ± 1.9 birds (N = 54, range = 2–10 birds). In all instances where an unassisted breeding pair successfully raised young (N = 3), the young remained with the parents and helped in the following years. In groups that have been observed for more than one year, all offspring have remained on natal territories and actively assisted the breeders. Therefore, the composition of a group includes the breeding pair and offspring aged one to several years old.

Territories.—The mean territory size was 42.1 ± 33.6 ha (N = 49, range = 9.4–104.0 ha). There was a significant difference between the sizes of territories located in the two study sites (Chamberlain-Auger, unpubl. data). The mean distance between nests in bordering territories was 0.86 ± 0.6 km (N = 12, range = 0.2–2.29 km).

Nests.—The mean nest depth was 24.1 ± 5.6 cm (N = 18, range = 10–38 cm). The mean nest diameter was 40.7 ± 6.6 cm (N = 19, range = 17–48 cm) and the mean nest cup diameter was 23.8 ± 4.5 cm (N = 17, range = 16–36 cm).

All of the nests were built in trees. The species of trees which were used were: pitch pine (*Pinus rigida,* N = 42), white pine (*P. strobus,* N = 2), spruce (*Picea* sp., N = 2), and eastern red-cedar (*Juniperus virginiana,* N = 2). The mean tree height was 11.0 ± 3.2 m (N = 44, range = 5.3–16.4 m). The mean nest height was 9.9 ± 3.1 m (N = 44, range = 4.6–15.4 m). In all cases new nests were built each year, and in some instances a second nest was built when the first failed.

We measured the distances between nests within a territory (crows remained on their territories year-round) for subsequent years and the mean intra-nest distance was 0.2 ± 0.2 km (N = 23, range = 0.0–0.6 km).

TABLE 1
GROUP SIZES OF AMERICAN CROWS

Year	Number per group									$\bar{x} \pm$ SD (N)
	2	3	4	5	6	7	8	9	10	
1983	—	3	—	1	—	—	—	—	—	3.5 ± 1.0 (4)
1984	2	7	1	2	1	—	—	—	—	3.5 ± 1.2 (13)
1985	1	4	4	2	3	—	—	—	—	4.1 ± 1.3 (14)
1986	—	6	2	2	2	1	3	—	—	4.9 ± 2.0 (16)
1987	—	3	—	1	—	1	—	1	1	5.7 ± 2.8 (7)
Total	3	23	7	8	6	2	3	1	1	4.4 ± 1.9 (54)

Incubation and brooding.—The mean incubation period for crows on Cape Cod (1983–1987) was 23.2 ± 6.0 days (N = 13, range = 14–33 days). We observed crows incubating during the months of March (N = 1), April (16), May (10), and June (2). The earliest date on which incubation was initiated was March 20, 1984, and the latest date on which we observed the beginning of incubation was June 17 (1985 and 1987). The months (N) during which hatching occurred or during which we observed young in the nest were: April (2), May (15), June (19), and July (1). The mean number of days until fledging was 29.6 ± 5.3 days (N = 15, range = 16–36 days). The earliest date on which we observed a nestling to fledge was May 26, 1985, and the latest was July 26, 1983.

Reproductive success.—Table 2 shows the mean number of fledglings that survived each year. Fig. 1 correlates group size with the number of surviving fledglings. There was no significant difference between fledgling survival and the number of birds in a group.

DISCUSSION

Group size.—American Crows were originally thought to have bred as pairs with the young dispersing at the end of the breeding season (Bent 1946, Good 1952, Goodwin 1976). Kilham (1984c) observed helping behaviors by auxiliaries and concluded that a cooperative breeding system was being employed by the Florida race of American Crows (*C. b. pascuus*). Our observations of the Cape Cod population concur with Kilham's findings. In addition our observations of particular behaviors in some of the groups suggest a trend towards communal breeding. We have observed shared incubation and brooding by breeders and helpers seven times in three years in the two largest breeding groups (unpubl. data). To date, all surviving offspring have remained on their natal territories for at least

TABLE 2
MEAN NUMBER OF SURVIVING FLEDGLINGS

Year	$\bar{x} \pm$ SD	No. nests
1983	0.8 ± 1.1	5
1984	2.3 ± 1.8	14
1985	2.0 ± 1.7	13
1986	3.3 ± 1.3	8
1987	1.0 ± 1.3	6
Total	2.0 ± 1.7	46

four years and acted as non-breeding helpers; consequently the group size increased each year.

Northwestern Crows also utilized a cooperative breeding system but only one of the offspring was allowed to remain as a helper each year (Butler et al. 1984). Another North American Crow, the Fish Crow (*C. ossifragus*) is not known to breed cooperatively (Goodwin 1976).

Territories.—Historically American Crows were thought to be non-territorial throughout most of the year except when nesting was occuring (Bent 1946, Good 1952, Goodwin 1976, Brown and Veltman 1987). Our observations revealed that the territories of crows on Cape Cod were all-purpose and actively defended throughout the year. Territorial behavior patterns described by Kilham (1985b) were observed for all group members, but in many instances the breeders initiated the displays with the auxiliaries joining later. During the coldest winter months, the crows from observed breeding groups joined other crows in a common roost. We observed the birds leaving their territories towards dusk, joining other crows in the roost throughout the night, and then returning to their territories at dawn.

The size of American Crow territory observed in our study area ranks between that of the Black Crow (*C. capensis*) (60 ha, Skead 1952) and the Carrion Crow (*C. corone*) (26.7 ± 10.4 ha, Wittenberg 1968). The nesting territory of the Northwestern Crow (0.49 ± 0.2 ha, Butler et al. 1984) is considerably smaller than American Crow territories observed in our study area.

Nests.—Nests of American Crows have been described in detail (Bent 1946, Good 1952). Nests were constructed by both the breeders and helpers (Kilham 1984, pers. obs.). In some cases, second nests were begun when the first failed. Renesting attempts have been reported by Emlen (1942) and Kilham (1986a). In addition to renesting, our observations

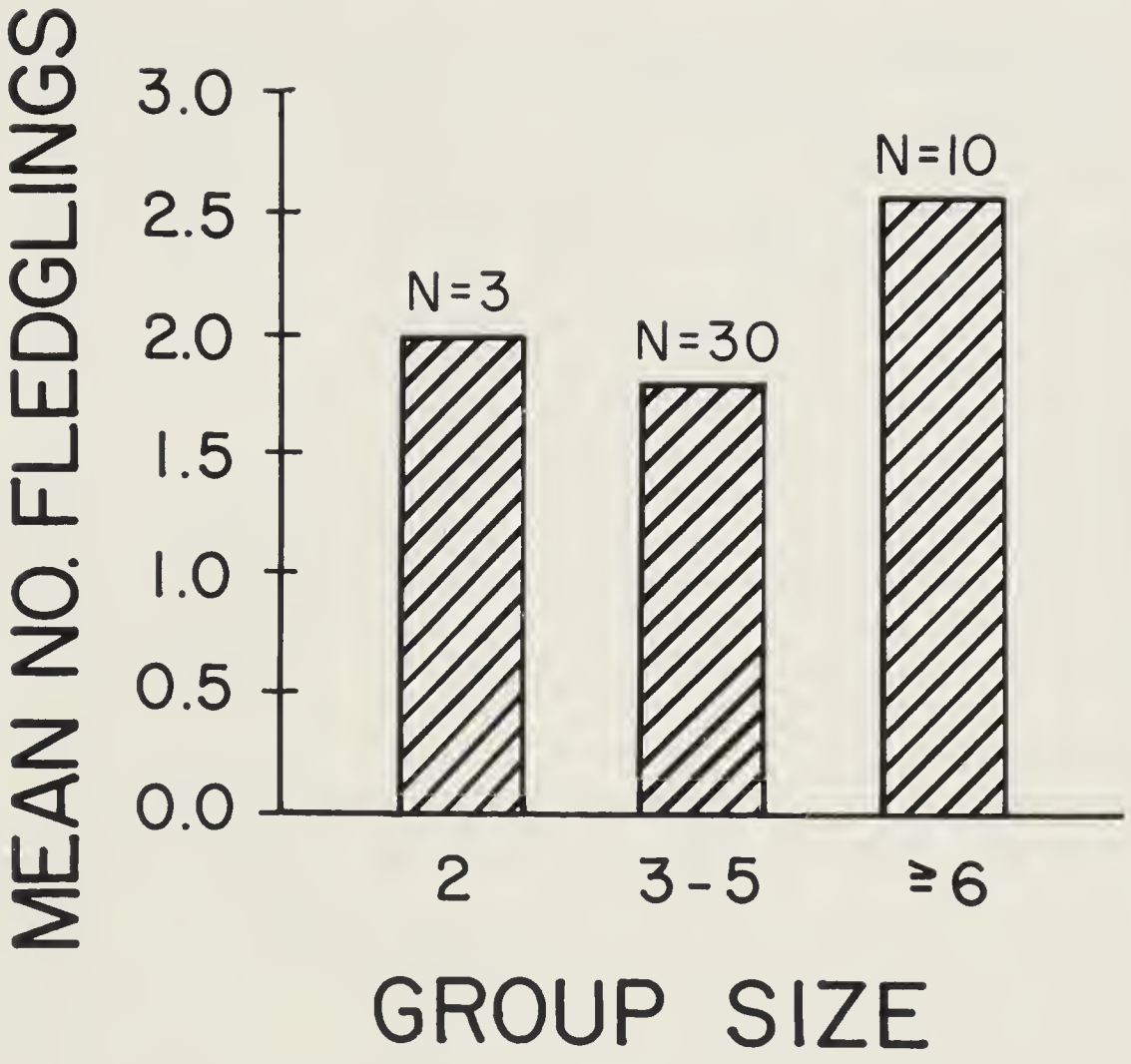

FIG. 1. Mean number of fledglings as a function of group size.

revealed the building of false nests or practice nests by both the breeders and the helpers. This was seen in 12 instances.

In some instances, Northwestern Crows build nests on the ground or in decidous trees (Butler et al. 1984) and there are reports of American Crows nesting in deciduous trees (Bent 1946, Good 1952). We found that all crow nests in our study area were in evergreen trees, with the majority of nests located in pitch pines, the most common tree in the area.

Incubation and brooding.—Reported incubation periods for American Crows vary from 16 days to 18 days (Emlen 1942, Bent 1946, Kilham 1984c). The breeding season for crows in Florida usually extends from January until May (Kilham 1985a). Good (1952) observed fledging to occur after 26 to 35 days, and Goodwin (1976) lists 35 days for *C. brachyrhynchos.* The average age of fledging for Northwestern Crows is 32 ± 2.5 days, and 26 ± 3.4 days (Butler et al. 1984). Incubation and brooding

in American Crows by the female exclusively has been observed by Good (1952) and Kilham (1984c), while incubation by both sexes was reported by Bent (1946). Our observations of crows on Cape Cod revealed incubation and brooding primarily by the breeding female but with assistance from the helpers (Chamberlain-Auger, unpubl. data). Feeding of the incubating bird and the young was a cooperative effort shared by the breeders and the helpers (Kilham 1984c, unpubl. data).

Reproductive success.—Emlen (1942) found 77% mortality of nestlings in a California colony of American Crows. Parental desertion and nestling competition were thought to be the causes of mortality. In our study, the known causes of mortality to eggs, nestlings, or fledglings were: predation by raccoons (*Procyon lotor*) (five nests containing nestlings) and Great Horned Owls (*Bubo virginianus*) (three nests with nestlings and one caged fledgling), automobiles (three fledglings), injury (one fledgling), infanticide (one nestling), hunting (one fledgling) (also discussed by Bent 1946 and Good 1952), starvation (two fledglings), and adverse weather conditions (one nest with nestlings). Butler et al. (1984) found a 75% survival rate of Northwestern Crow fledglings after nine weeks. Glaucous-winged Gulls (*Larus glaucescens*) were the primary cause of fledgling deaths.

Woolfenden and Fitzpatrick (1984) examined the effect of helpers on reproductive success in Florida Scrub Jays (*Aphelocoma c. coerulescens*). Their results showed a significant increase in fledgling success when a helper was present but no increase in production as helper numbers increased. In addition, they observed a trend towards increased fledgling success when an older, experienced helper was present. Similarly, Lawton and Guinton (1981) reported a significant increase in Brown Jay (*Cyanocorax morio*) fledgling production with experienced helpers.

In our study, there was no significant difference in fledgling production between groups without any helpers and groups with one to three helpers, although the trend was for decreased production in the larger group size. We propose that this trend can be explained as a consequence of habitat variation between territories which resulted in subsequent mortality differences. We observed an increased degree of predation on eggs and nestlings of groups living in the more rural undeveloped areas (N = 12 or 40%), i.e., the barrier beach. The result was fewer fledglings surviving ($\bar{x}$ = 0.6 ± 1.4). Two of the causes of the increased predation rate on the rural groups were lower nest heights and a lack of a food source provided by humans (garbage and road kills). We suspect that raccoons, the most common predator, were forced to search for natural foods and had greater access to crow nests (unpubl. data).

In groups greater than or equal to six birds (four or more helpers), there was a trend towards increased fledgling production. All of these groups

were found in the more urban regions of the study site, and all contained experienced helpers. In addition, our observations have revealed that in a few of the largest groups one-year-old birds, the inexperienced helpers, were permitted to watch the breeders and older helpers but not allowed to participate in the feeding of the incubator/brooder or nestlings.

American Crows were initially thought to have a simple breeding system but our observations are similar to recent studies revealing the more complex reproductive system of a highly social bird.

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DOMINANCE RANK AND RESOURCE ACCESS IN WINTER FLOCKS OF BLACK-CAPPED CHICKADEES

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ABSTRACT.—We investigated the relationship between dominance rank and access to a winter feeding station in Black-capped Chickadees (*Parus atricapillus*). Although there was considerable inter-individual variation, dominance rank was not strongly related to number of visits to the feeder or length of visit. Because dominants were more likely than subordinates to approach a bird on the feeder, dominants tended to have access to the feeder at any time, while subordinates had to wait for the feeder to be unoccupied. Dominant individuals were involved in more agonistic encounters than subordinates. Interactions occurred between high-ranking individuals more often than expected by chance, while middle-ranking birds interacted less often than expected with individuals of all ranks. Birds also interacted more than expected with members of their own flock and less often with members of other flocks.
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Dominance hierarchies occur in many species, yet the costs and benefits of holding a particular rank are not always clear (Huntingford and Turner 1987). Among birds forming flocks, dominants have been shown to benefit by increased access to food resources (Baker et al. 1981, Ekman and Askenmo 1984, Poysa 1988, Hogstad 1989) or to locations safest from predators (Schneider 1984, Hegner 1985, Ekman 1987, Desrochers 1989, Hogstad 1989). Potential costs to dominants include increased rates of aggression (Rohwer and Ewald 1981) or higher metabolic rates (Røskaft et al. 1986, Hogstad 1987). In this study, we examined some of the costs and benefits of dominance among Black-capped Chickadees (*Parus atricapillus*) in winter flocks. We tested the following hypotheses: (1) Higher-ranking birds have greater access than lower-ranking birds to an artificial point source of food; and (2) Higher-ranking birds face increased costs, as measured by number of agonistic encounters (Hogstad 1989). In addition, we investigated whether individuals interacted with each other at random or if they interacted with certain individuals more than others.

METHODS

We made observations at a feeder at the University of Wisconsin–Milwaukee Field Station, Saukville, Ozaukee County, Wisconsin (a site described by Weise and Meyer 1979), from 27 November 1982 to 24 March 1983. The feeder was always available to the chickadees from 15 November 1982 until 1 May 1983.

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The feeder was designed to facilitate observation of aggressive encounters. It had two perches 23 cm apart and projecting 5.5 cm from the front of the feeder. Between the perches was a single entrance to a chamber enclosed by wire mesh, within which the sunflower seed hopper was located. Only one bird entered the feeder at a time and usually stayed only long enough to select a seed, which was then carried away from the feeder. Agonistic encounters took place on the two perches or with one bird on a perch and the other inside the feeder. Birds could take their seed either from the hopper or from the floor of the feeder. Seeds on the floor were usually ones that had been dropped and may have been inferior in quality.

The chickadees were individually color banded as part of a long-term study of this population by CMW. We knew the sex and ages of most adult birds. We recognized first-year birds by skull ossification (August–November) or by shape of rectrices (Pyle et al. 1987). We tentatively sexed these birds by wing chord length (Weise 1979); we confirmed or more rarely corrected by sex-specific behavior the sex designations of those individuals that later entered the breeding population (Weise 1979). We attempted to note the color bands of all birds visiting the feeder during videotaping, although this was not always possible.

We videotaped all observations using a Sony video camera equipped with a Nikon lens. The observer and camera were concealed in a blind 10 m from the feeder, and we turned the camera on whenever chickadees were in the vicinity of the feeder. Between 0900 and 1200 CST, we videotaped four, 33 min tapes each week, with two tapes per day of observations, for a total of 82 tapes.

The video tapes were later rerecorded with a timer on the tape (recording to 0.01 sec). We noted the time each bird arrived at the feeder, whether or not it obtained a seed, whether that seed came from the hopper or the floor, and the departure time of the bird. If an aggressive encounter occurred, we noted the winner and loser. An aggressive encounter was said to have occurred when one bird supplanted another at the feeder or two chickadees gave an exchange of postures and/or calls with one bird eventually gaining access to the seeds. We defined the winner as: (1) the first bird to obtain a seed, or (2) in the rare cases when neither bird obtained a seed, the last bird to leave the feeder.

We analyzed 7126 visits to the feeder, during which 1200 interactions occurred. To ensure a sample size large enough for comparisons among individuals, we selected for analysis 20 individuals that visited the feeder at least 80 times (Table 1). The individuals chosen for analysis were from four different flocks, and included both males and females. We determined the dominance hierarchy by ranking individuals so as to minimize the number of losses to individuals ranked higher. Using the number of individuals dominated to determine the dominance hierarchy produced an identical hierarchy.

For each individual, we determined the number of times it visited the feeder, the number of encounters in which it was involved, the percentage of visits in which it had an agonistic encounter, and the mean duration of its visit from the time it arrived at a perch. In addition, we noted the percentage of visits in which each individual obtained a seed, and the percentage of seeds taken from the floor (as opposed to the hopper). We also determined for each individual the percentage of visits to the feeder in which that individual approached a bird already present there, and the percentage in which that individual was on the feeder and was approached by another bird. We used Spearman rank correlations to compare dominance rank and each of these measures for all individuals, and separately for males and for females. Correlations with a $P < 0.05$ were considered significant.

To investigate whether individuals interacted with certain individuals more than expected by chance, we assumed that the number of times individuals visited the feeder reflected the opportunities those individuals had to interact with each other. We calculated the expected number of interactions between any two individuals from the number of visits each individual made. The expected number represented the number of encounters expected if in-

TABLE 1

THE SEX, AGE AND FLOCK MEMBERSHIP FOR EACH BLACK-CAPPED CHICKADEE IN THE STUDY, LISTED FROM HIGHEST TO LOWEST RANKING INDIVIDUAL (TOP TO BOTTOM)

Individual	Sex	Hatch year	Flock No.
1	Male	1980	1
2	Male	1981	1
3	Male	1982	1
4	Male	1981	1
5	Male	1980	1
6	Male	1982	1
7	Male	1982	2
8	Male	1981	3
9	Male	1979	3
10	Female	1982	1
11	Male	1982	3
12	Female	1980	1
13	Male	1982	1 or 4?
14	Female	1978	2
15	Female	1982	1
16	Female	1981	3
17	Female	1982	3
18	Female	1980	1
19	Male	1982	1
20	Female	1981	4

dividuals interacted at random. Expected values were calculated for each tape and then summed for all tapes. We grouped individuals as high-ranking (birds 1–7), middle-ranking (birds 8–13), or low-ranking (birds 14–20). We compared observed and expected numbers of interactions within and between each dominance group. We also compared observed and expected numbers for interactions between individuals of the same flock versus individuals of different flocks and for encounters between males, between females, and between males and females. We made these comparisons of observed and expected values using the *G*-statistic for goodness-of-fit. To detect trends among individuals, we calculated Freeman-Tukey deviates (Sokal and Rohlf 1981). Deviates greater than two or less than negative two suggest significant differences between observed and expected values.

RESULTS

Access to food.—The number of visits made by each individual to the feeder varied greatly (extremes: 83–814). The number of visits was significantly correlated with rank (Fig. 1, all individuals, $r_s = 0.44$) but only because of the high number of visits made by birds 6 and 7. When males and females were considered separately, the correlations were not significant for either group ($r_s = 0.27$ and 0.13, respectively). The mean time the individual spent on the feeder per visit was not significantly correlated

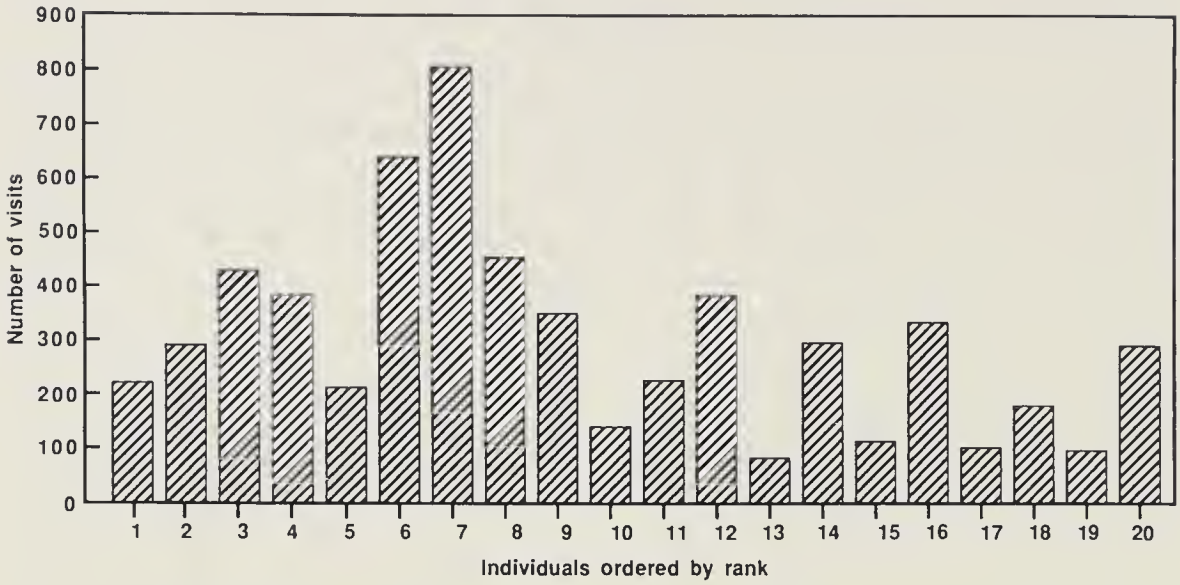

FIG. 1. Number of visits made to the feeder by each individual.

with rank (for all individuals, $r_s = -0.24$; males only, $r_s = -0.45$; females only, $r_s = -0.26$). For most individuals, the mean visit time was between 4.0 and 5.5 sec.

All individuals obtained seeds in most of their visits to the feeder (in 80% to 100% of visits). Accordingly, rank was not significantly correlated with percentage of visits in which a seed was obtained (for all individuals, $r_s = 0.27$; for males only, $r_s = 0.35$; for females only, $r_s = -0.02$). Chickadees could obtain seeds from the hopper or from the floor of the feeder. Rank was not correlated with the percentage of seeds taken from the floor

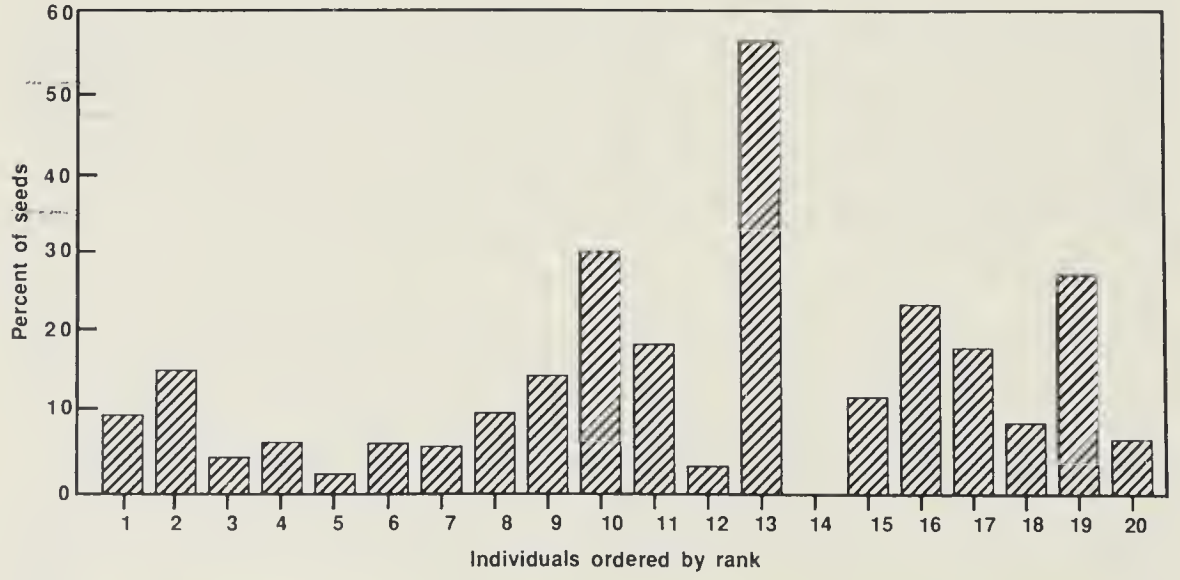

FIG. 2. Percent of seeds that each individual obtained from the floor of the feeder.

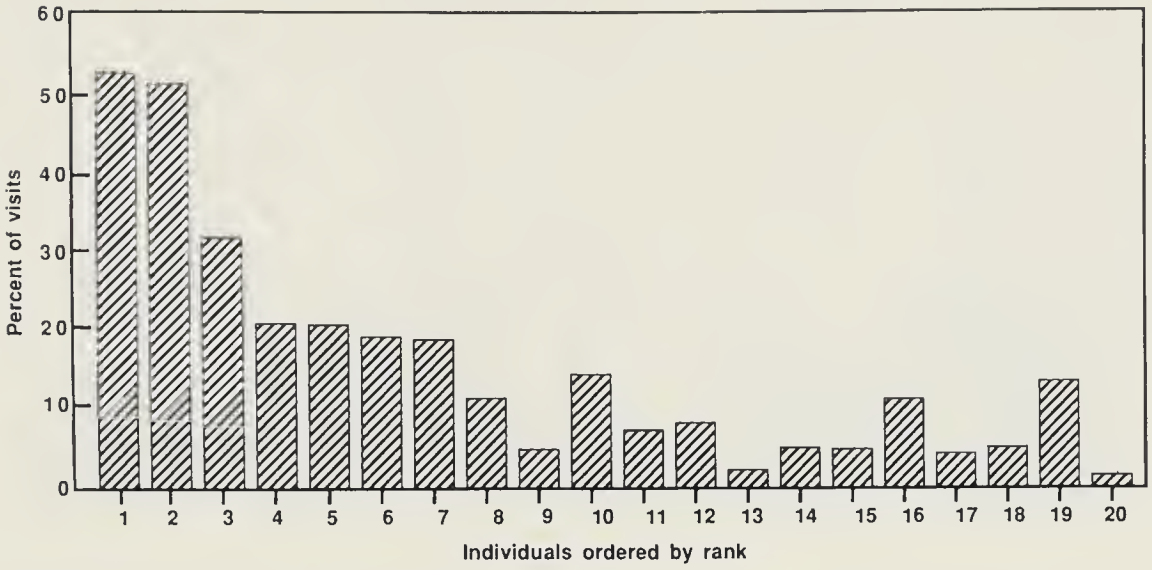

FIG. 3. Percent of visits in which each individual approached the feeder when another bird was already present on the feeder.

(Fig. 2, $r_s = -0.29$). Most of the birds that took more than 20% of their seeds from the floor were, however, in the lower half of the dominance hierarchy. The absence of a significant correlation was due to the considerable variation among these low-ranking birds. This correlation was significant when males were considered alone ($r_s = -0.57$).

One potential advantage of taking a seed from the floor rather than the hopper would be a reduced time spent at the feeder. To test this hypothesis, we used a paired t-test to compare for each individual the time spent per visit when a seed was obtained at the hopper versus when a seed was obtained from the floor. This comparison was nonsignificant ($t = 1.13$, $df = 18$, $P > 0.05$).

Priority to food.—The percentage of visits in which an individual approached a bird on the feeder (as opposed to visits when the feeder was unoccupied) was correlated with rank (Fig. 3, $r_s = 0.89$). Dominant birds were more likely than subordinate birds to visit when a bird was on the feeder. This correlation was significant for both males ($r_s = 0.90$) and females ($r_s = 0.67$). In contrast, there was no significant correlation between rank and the percentage of visits in which an individual was approached while on the feeder (Fig. 4, for all individuals, $r_s = -0.28$; for males, $r_s = -0.13$; for females, $r_s = 0.33$).

Encounters.—The number of encounters in which each individual was involved was significantly correlated with rank (Fig. 5, all individuals, $r_s = 0.68$). Higher ranking birds were involved in more encounters than lower ranking birds. This comparison was significant for males ($r_s = 0.64$), but not for females ($r_s = 0.55$). The percentage of visits in which there

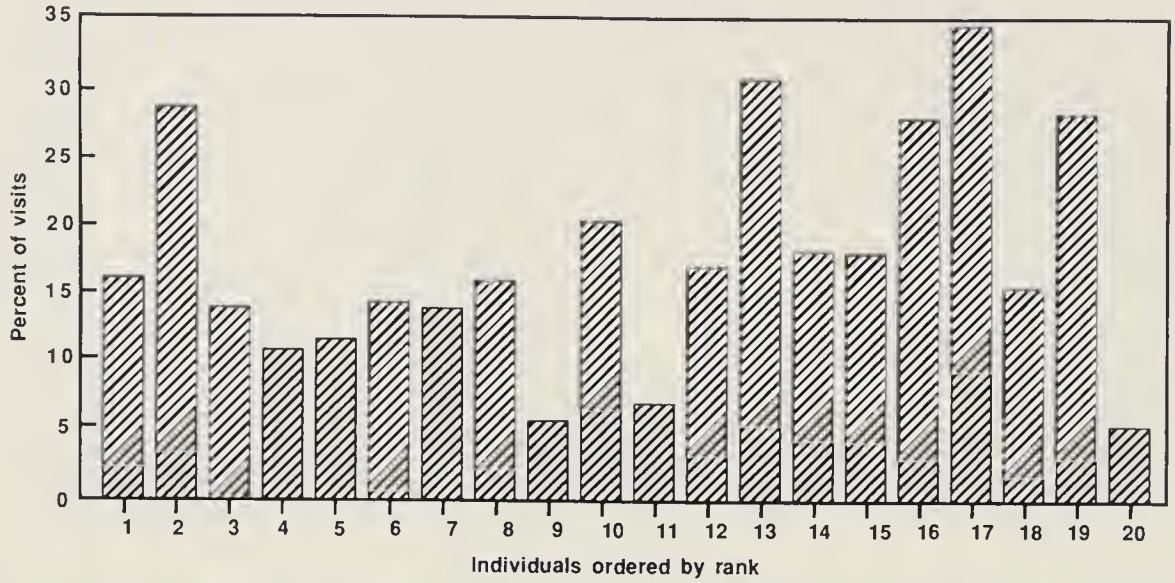

FIG. 4. Percent of visits in which each individual was approached by another bird while they were on the feeder.

were encounters was also significantly correlated with rank (Fig. 6, r_s = 0.44). This significant correlation was due to the high percentages for the two most dominant birds. Again this comparison was significant for males (r_s = 0.51), but not for females (r_s = 0.40).

Observed and expected numbers of encounters within and between dominance groups were significantly different (Table 2, G = 127.4, df = 5, $P < 0.001$). Interactions were more frequent than expected among high-ranking birds, while middle-ranking birds interacted less than expected with individuals of all ranks. Individuals also interacted with mem-

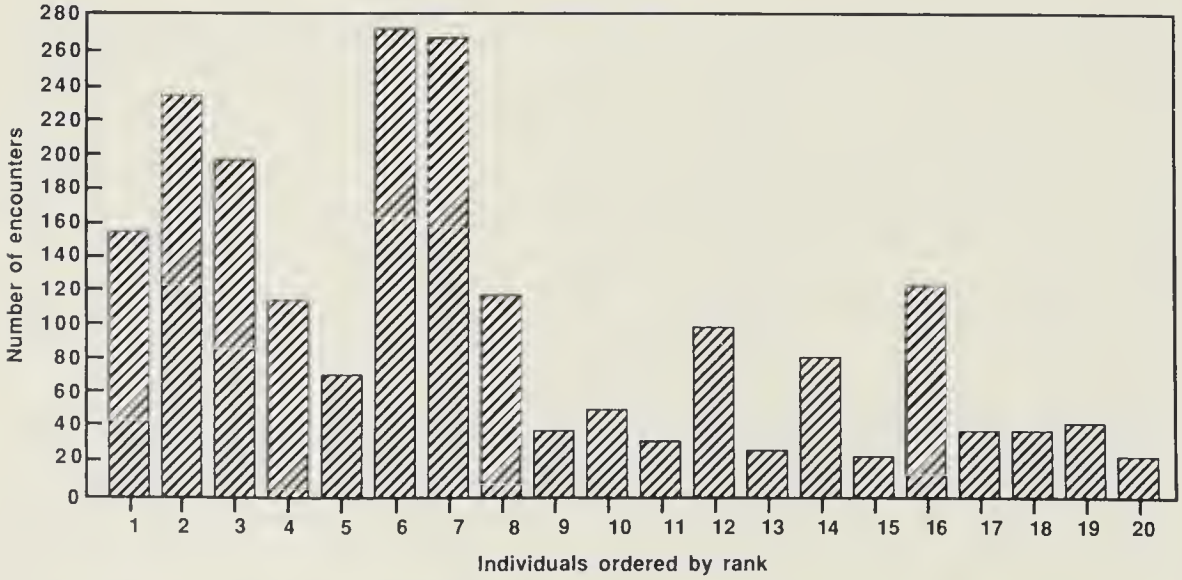

FIG. 5. Number of agonistic encounters in which each individual was involved.

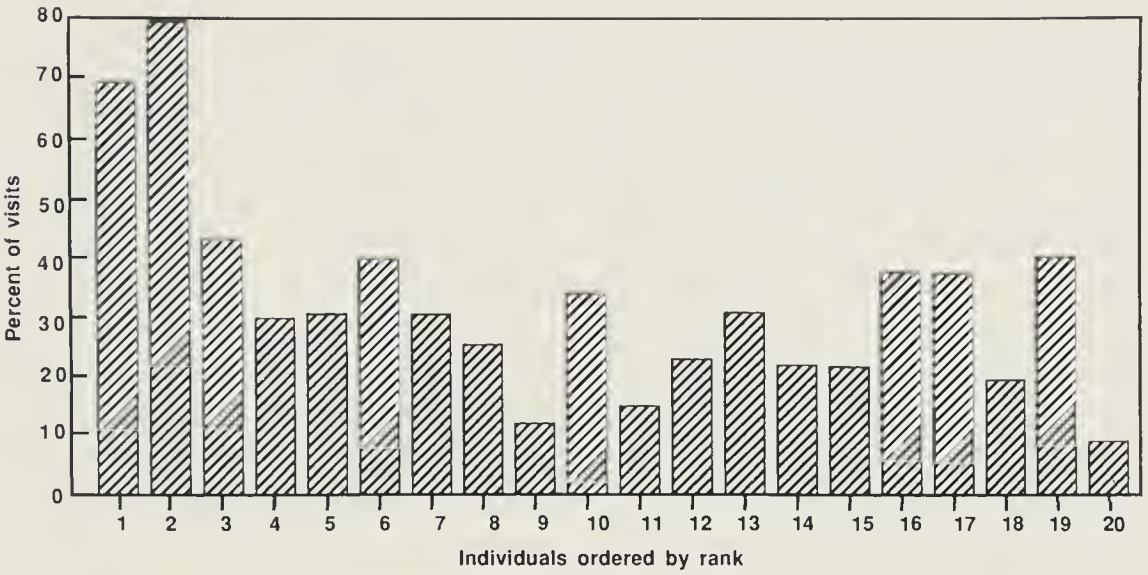

FIG. 6. Percent of visits to the feeder in which each individual was involved in an agonistic encounter.

bers of their own flock more than expected and with members of other flocks less than expected (members: obs 432, exp 262; non-members: obs 342, exp 513; $G = 156.2$, $P < 0.001$). Interactions among males were more frequent than expected, while females interacted less than expected with both males and other females (Male-male: obs 417, exp 378; female-female: obs 31, exp 53; female-male: obs 326, exp 347; $G = 16.1$, df = 2, $P < 0.001$).

Comparisons of rank, sex, and flock membership are not independent (i.e., most high-ranking birds are males from flock 1). To avoid this lack of independence, we compared observed and expected values on an individual basis using Freeman-Tukey deviates. Significant positive deviates (observed values greater than expected) were most commonly asso-

TABLE 2

OBSERVED AND EXPECTED NUMBER OF INTERACTIONS BETWEEN AND WITHIN EACH DOMINANCE GROUP

Dominance rank of contestants	Observed	Expected
High-high	302	179
High-middle	163	229
High-low	188	178
Middle-middle	22	53
Middle-low	81	105
Low-low	18	30

ciated with the two highest ranking birds. Particularly high deviates were found for interactions between birds 1 and 2 and for interactions birds 1 and 2 had with birds 3, 6, and 7. Significant negative deviates were mostly associated with interaction among middle-ranking birds (especially birds 9, 11, and 12). Bird 9 interacted with other birds much less than expected; 15 of 19 deviates were negative (6 were significant).

Male-female differences.—We compared mean values of males with those of females for the eight measures described above. We found significant differences for only two measures: number of encounters and percentage of times an individual approached a bird on the feeder. Males were more than twice as likely as females to be in an encounter (males: $\bar{x} = 130.1$, females: $\bar{x} = 60.4$, t for unequal variances = 2.36, $P < 0.05$). Males also approached a bird in a greater percentage of their visits to the feeder (males: $\bar{x} = 21.2\%$, females: $\bar{x} = 6.4\%$, t for unequal variances = 2.93, $P < 0.05$).

DISCUSSION

Dominance has previously been reported to affect foraging in winter flocking birds. High-ranking birds may have greater access to food resources (Ekman and Askenmo 1984, Enoksson 1988, Hogstad 1988) or face reduced risk of predation (Schneider 1984, Hegner 1985, de Laet 1985). A relationship between rank and access to feeding sites has been previously suggested for Black-capped Chickadees (Glase 1974), and Desrochers et al. (1988) have shown a positive relationship between rank and winter survival. In this study, we found considerable individual variation in access to a super abundant, highly concentrated food source, but this variation was not strongly related to rank. As the chickadees obtained a seed in most of their visits and as their visits varied little in length, the number of visits to the feeder was a good indicator of resource access. There was nearly a ten-fold difference among individuals in number of visits. The highest numbers of visits, however, were made by middle-ranking males (birds 6 and 7), while the two highest-ranking birds made fewer visits than some low-ranking birds (i.e., 14, 16, and 20). Poysa (1988) also reported large variation among individual Great Tits (*P. major*) in their visits to a feeder. In that study, however, resource access was related to dominance rank.

Despite not having greater access to the feeder, high-ranking birds were involved in more agonistic encounters than low-ranking birds. Why did dominants pay a cost (increased encounters) to maintain their high rank, without a compensatory benefit of increased resource access? The costs of being in an agonistic encounter may have been low. Actual physical fights were not observed, although encounters were often long with several exchanges of displays (Popp et al. 1990). Maintaining a high rank may

also have provided benefits: (1) away from the feeder, (2) later during the breeding season, or (3) during times of severe weather when access to the feeder may be more important (Brittingham and Temple 1988).

High-ranking birds did have an advantage in being able to approach the feeder at any time, while low-ranking birds were more likely to wait until the perches were unoccupied. At natural food sources that are quickly depleted (i.e., a seed head on a plant or a leaf with insect eggs), this may give high-ranking birds a definite advantage. In addition, by having to wait near the feeder for access to it, subordinates may be in more exposed positions and face higher rates of predation (Lima 1985, Waite 1987, Poysa 1988). Subordinates also have to wait for access to feeders in social groups of Scrub Jays (*Aphelocoma coerulescens*) (Craig et al. 1982).

By using the number of visits to the feeder as a measure of the opportunity individuals had to interact with one another, it was possible to test whether or not individuals interacted with each other in a random pattern. The suggestion that high-ranking birds were involved in more encounters than lower-ranking ones is supported by the greater than expected number of encounters among high-ranking birds. In general, middle-ranking birds were involved in fewer encounters than expected; this fact is also supported by examination of individual deviates. Flock membership also affected frequency of interactions, with individuals being more likely to interact with flock members than members of other flocks. This result may indicate that it is most important for individuals to maintain dominance relationships with members of their own flocks. It is important to note that these comparisons (rank, flock membership, and sex) are not independent. An examination of individual deviates suggests that the larger than expected number of encounters among males and among flockmates may have been due to the large number of observed interactions among the three highest ranking birds (males from flock 1).

The results of this study may have been affected by the feeder being within the home range of flock 1. The six highest-ranking birds were from flock 1, although the other individuals from flock 1 were distributed throughout the dominance hierarchy. Birds from flock 1 did not appear to visit the feeder more than ones from the other flocks. A bird from flock 2 was the most frequent visitor to the feeder and some individuals from flock 3 (i.e., birds 8, 9, and 16) were frequent visitors. Members of different flocks often visited the feeder at the same time as demonstrated by the large number of aggressive encounters between different flock members.

ACKNOWLEDGMENTS

We thank L. Bunkfeldt-Popp, J. Ekman and A. Dhondt for their comments and J. Reinartz for his assistance with computer programming. Contribution No. 123 of the University of Wisconsin–Milwaukee Field Station.

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NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANT AWARDS 1990

The North American Bluebird Society is pleased to announce the presentation of the seventh annual research grant awards. The 1990 recipients are as follows:

BLUEBIRD GRANTS

DR. JANIS L. DICKINSON, Hastings Natural History Reservation, Carmel Valley, California. Topic: Use of DNA fingerprinting to determine paternity in Western Bluebird nests.

KEVIN L. BERNER, State University of New York, College of Agriculture and Technology, Cobleskill, New York. Topic: Field tests of acceptance of Eastern Bluebirds of nest boxes which deter raccoon predation.

GENERAL GRANTS

DR. MICHAEL J. DEJONG, Department of Biology, College of St. Thomas, St. Paul, Minnesota. Topic: Indirect effects of the larvicide *Bacillus thuringiensis* on Tree Swallow breeding success.

CHARLOTTE C. CORKRAN, Northwest Ecological Research Institute, Portland, Oregon. Topic: Reproductive success of Western and Mountain Bluebirds in grasshopper control areas, and potential for using bluebirds to reduce grasshopper densities.

STUDENT GRANTS

SUSAN MEEK, Biology Department, Queen's University, Kingston, Canada. Topic: Parental investment and the maintenance of monogamy in Eastern Bluebirds.

JONATHAN H. PLISSNER, Department of Biological Sciences, Clemson, University, Clemson, South Carolina. Topic: Does social dominance drive natal dispersal in Eastern Bluebirds?

The North American Bluebird Society annually provides research grants in aid for ornithological research directed towards cavity nesting species of North America with an emphasis on the genus *Sialia*. Information and application materials are available from Kevin Berner, Research Committee Chairman, College of Agriculture and Technology, State University of New York, Cobleskill, New York 12043.

Wilson Bull., 102(4), 1990, pp. 634–644

INFLUENCE OF FOREST EDGE ON NEST-SITE SELECTION BY TREE SWALLOWS

WALLACE B. RENDELL AND RALEIGH J. ROBERTSON[1]

ABSTRACT.—We examined the influence of forest edge on nest-site selection by Tree Swallows (*Tachycineta bicolor*) at nest-box grids in uniform habitats. Tree Swallows occupied nest sites at distances of 3–100 m from forest edge, while House Wrens (*Troglodytes aedon*) and most Eastern Bluebirds (*Sialia sialis*) used boxes within 30 m of forest edge. Mean distance to forest edge for the distribution of nest boxes used by Tree Swallows was greater than those means for Eastern Bluebirds and House Wrens, but mean distances to forest edge for nest boxes occupied by the latter two species were not different. Partial correlation analysis showed that settlement dates at nest boxes by single Tree Swallows (often known to be males), and dates of pair formation, were correlated negatively with distance to forest edge (i.e., Tree Swallows settled first at nest boxes that were farthest from forest edge). Also, when a pair of Tree Swallows had a choice of more than one nest box in which to breed (i.e., their territory included more than one nest box), they selected most frequently the nest box farthest from forest edge. Whereas predation by raccoons (*Procyon lotor*) and black rat snakes (*Elaphe obsoleta*) at Tree Swallow nest boxes occurred at distances from forest edge up to 80 m, House Wrens destroyed eggs and usurped nest boxes from Tree Swallows only within 20 m of forest edge. Further, although Eastern Bluebirds did not usurp nest boxes from Tree Swallows, both species are known to compete aggressively for boxes. Therefore, Tree Swallows may select nest sites farther from forest edge to avoid the costs of aggression or nest destruction that may be incurred during interactions with competitors, especially House Wrens. *Received 8 Sept. 1989, accepted 20 Feb. 1990.*

Nest-site selection by secondary cavity-nesting birds is an important determinant of fitness because several characteristics of nest sites can influence reproductive success. For example, cavity height influences success since lower cavities are more susceptible to predation (Nilsson 1984, Rendell and Robertson 1989). Also, clutch size is positively influenced by cavity size for many species (Karlsson and Nilsson 1977, Rendell and Robertson 1989). Further, habitat cover and foliage density influence fledging success for House Wrens (*Troglodytes aedon*) which are better able to detect and deflect predators in sparsely foliated vegetation than in dense vegetation (Finch 1989).

In this study we examined the influence of distance to forest edge on nest-site selection by Tree Swallows (*Tachycineta bicolor*). Observations of settling patterns of Tree Swallows breeding in grids of nest boxes gave the general impression that early settling pairs avoided boxes near forest edge. Subsequently, boxes near forest edge were often occupied by House

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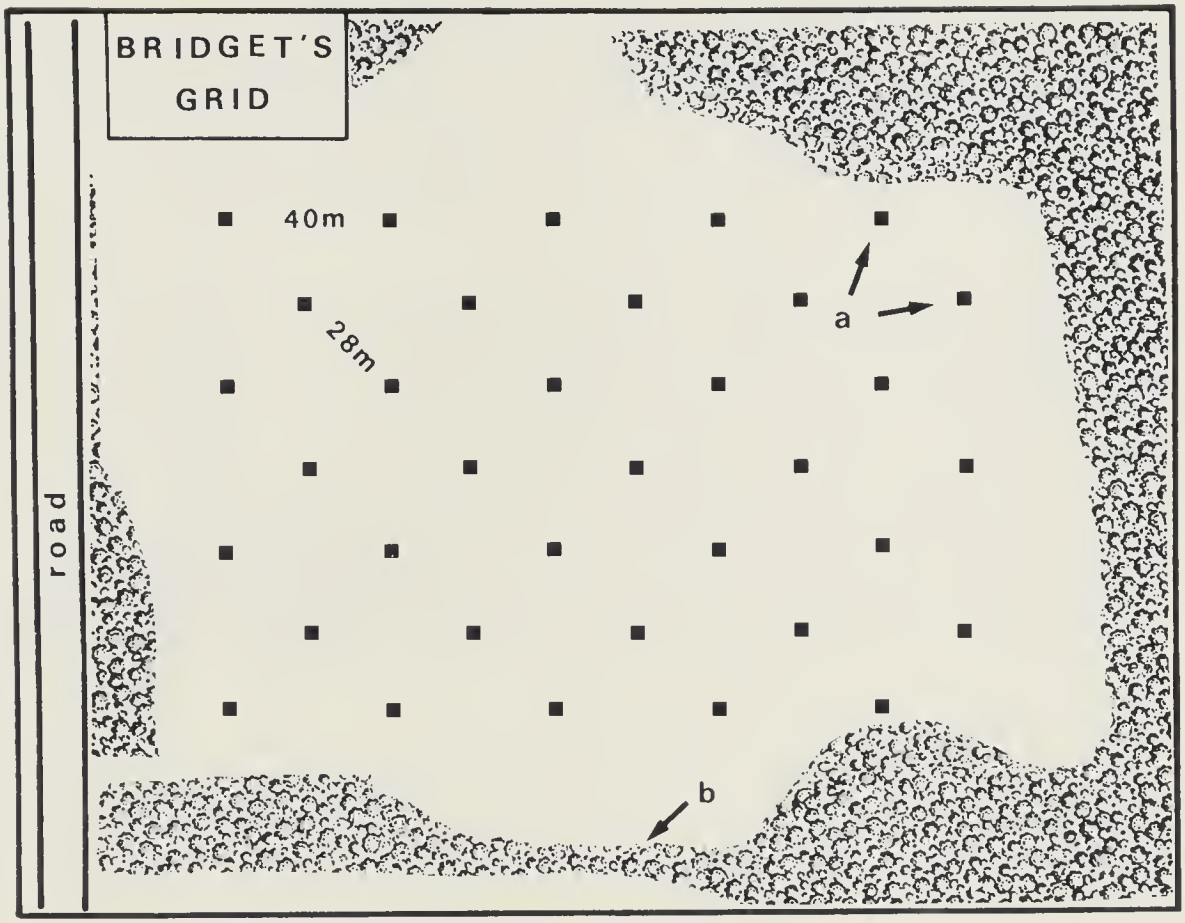


FIG. 1. Scale diagram of Bridget's Grid showing the arrangement of boxes in a grid, boxes at the grid edge (a), and forest edge (b).

Wrens and Eastern Bluebirds (*Sialia sialis*). Here we quantify those settling patterns and the distribution of nest failures caused by predation and nest-box usurpation and argue that Tree Swallows prefer to nest farther from forest edge to avoid interference from competing species, especially House Wrens.

STUDY AREA AND METHODS

Data were collected from 1986–1989. Three species (Tree Swallows, Eastern Bluebirds, and House Wrens) bred at grids of nest boxes located in four hayfields (Bridget's Grid [Fig. 1], BG; Hughson's Grid, HU; New Barn Grid, NB; and Sand Pit Grid, SP) on research tracts of the Queen's University Biological Station, Chaffey's Lock, Ontario. The hayfields ranged in size from 0.8–2.8 ha, and all four fields were situated within 0.8 km of each other. Three fields (BG, NB, and SP) were bordered on at least three sides by deciduous forest edge consisting primarily of poplar (*Populus* spp.), maple (*Acer* spp.) and oak (*Quercus* spp.). Hughson's Grid was bordered more distantly on two sides by forest and on two sides by field and marsh.

An abundant supply of nest sites (N = 77) was available at each grid in each year (BG, 35; HU, 18; NB, 14; and SP, 10), with additional nest sites available at three grids in 1986

only (BG, 3; NB, 1; and SP, 1). Nest boxes were mounted on aluminum poles (1.5–2.0 m high) arranged in columns and rows throughout each field; the distance between nearest boxes in a row or column was 40 m, and the distance along the diagonal was 28 m (Fig. 1). All nest-box entrances faced east, and all boxes and entrances were standard size (cavity volume = 3897 cm^3, entrance diameter = 3.7 cm), except in 1989 when the volume of boxes on alternate nest sites at BG was reduced by half (ca 1700 cm^3) as part of a separate study.

At alternate nest sites at HU (1987–1988) and BG (1987–1989), a second nest box was situated 8 m from the original box (i.e., boxes were paired), again as part of a separate study. We use the term nest site to refer to the physical cavity in which a pair nests (i.e., focal box), as well as the habitat surrounding a focal box. Since Tree Swallows usually defend territories with a radius of at least 10 m around a focal box (Robertson and Gibbs 1982, Muldal et al. 1985) we consider each of the sites with paired boxes as a single nest site because simultaneous use of the remaining box by another species or conspecific pair was precluded in most cases. Simultaneous occupancy of both of a pair of boxes either by different species or different breeding pairs occurred only 6 of 72 (8%) possible times. Thus, sample sizes indicate the number of nest sites available. Although most Tree Swallows defended only one nest site (either a single box or pair of boxes within 8 m) some initially defended larger territories which encompassed more than one nest site (i.e., single or paired boxes 28–40 m apart).

Surveys at all grids from late March to August throughout each breeding season enabled us to map which nest sites were used by a given species. A nest site was occupied when a species attempted to breed at the site (e.g., nest-building, egg laying, etc.), and also when a species actively prevented competitors from access to a box, either through territorial defense (e.g., Tree Swallows) and/or by nest-building (e.g., dummy nests of male House Wrens; cf, Finch 1989). The distances from the focal box in a territory to the nearest forest edge, and to the nearest grid edge (Fig. 1), were measured. Nest sites that were located along the periphery of a grid were defined as being on the grid edge, and therefore, the distance of a focal box on these nest sites to the grid edge was zero.

For Tree Swallows, settlement dates at nest sites at the two largest grids (BG and HU) were recorded by doing daily scans of the grids (cf, Stutchbury and Robertson 1987a) from the time of arrival of the first birds in late March or early April until most nest sites were occupied and nesting was underway in early May. In 1986, data were available for settlement dates of pairs, while in 1987–1989, settlement dates of both single individuals (often known to be males) and pairs were available.

RESULTS

Occupancy.—Tree Swallows occupied the vast majority of available nest sites at all grids during the study (N = 294; Fig. 2). House Wrens occupied 18 nest sites, mostly at BG and SP. House Wrens were common from 1986–1988, but only one pair nested at BG in 1989. House Wrens never bred at HU grid. Eastern Bluebirds also occupied nest sites at all grids in each year (N = 26). Nest-site occupancy rates were high in all years at each grid (range 93–100%), and all nest sites were used at some time during the study. Twenty-one nest sites were used twice (and were therefore considered to be available twice), and four nest sites were used three times (and were therefore available three times) in a given year,

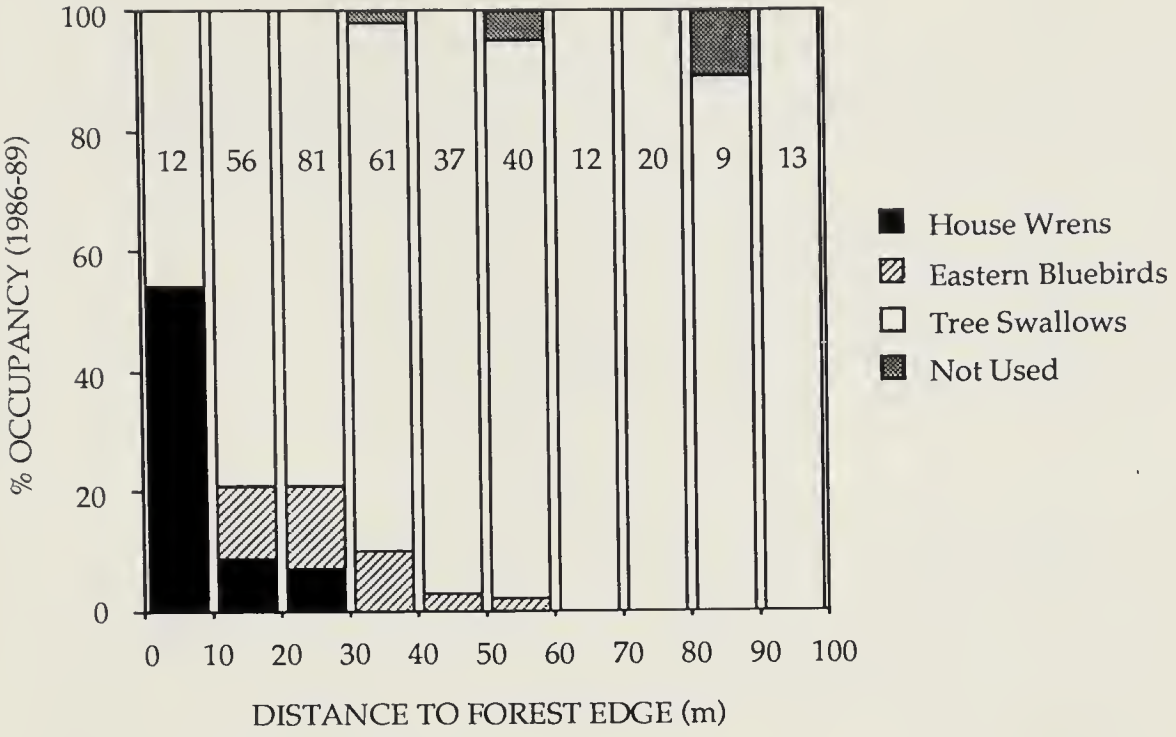
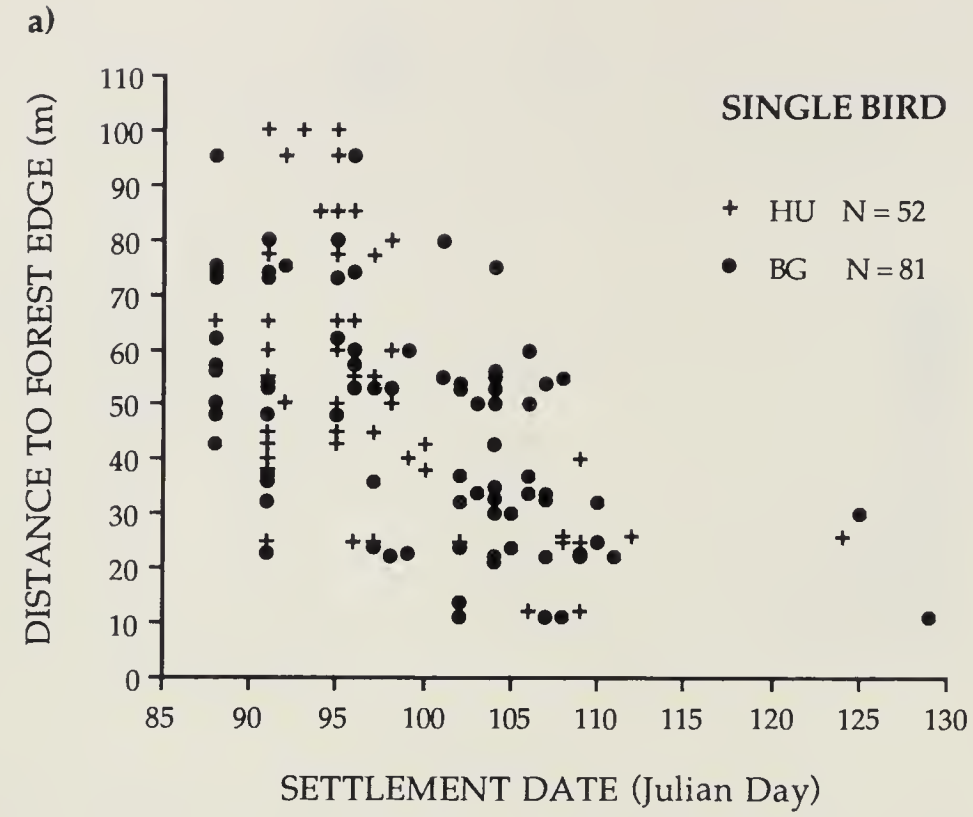


FIG. 2. Distribution of nest sites used by Tree Swallows, House Wrens, and Eastern Bluebirds, and those not used, relative to distance to forest edge (1986–1989). Sample sizes of the number of nest sites available for use are presented within each distance cell.

often by different species; hence, the total number of nest sites used by all three species combined (N = 338) was greater than the number of available nest sites throughout the study (N = 313).

House Wrens occupied nest boxes close to forest edge (range 3–30 m). Most Eastern Bluebird pairs (69%; 18/26) also nested less than 30 m from forest edge, but the range of distances from forest edge for this species (10–53 m) was greater than that for House Wrens. Tree Swallows occupied boxes at all distances from the surrounding edge (range 3–100 m), and only this species used boxes greater than 60 m from forest edge (Fig. 2). Mean distances to forest edge for distributions of nest boxes used by House Wrens ($\bar{x}$ = 13.9 ± 2.2 [SE] m, N = 18) and Eastern Bluebirds (25.8 ± 2.2 m, 26; Tukey HSD Multiple Comparison, $q_{[0.05]} = 2.55$, df = 335, $P > 0.05$) were not different. Mean distances to forest edge for nest boxes of House Wrens and Tree Swallows (41.3 ± 1.3 m, 294; Tukey HSD, $q = 7.40$, df = 335, $P < 0.05$), and Eastern Bluebirds and Tree Swallows (Tukey HSD, $q = 4.96$, df = 335, $P < 0.05$), were different.

Forest edge avoidance by Tree Swallows.—Settlement dates of Tree Swallows at nest sites in BG and HU from 1986–1989 were negatively correlated with distance to forest edge and distance to grid edge (Table 1). Nest sites farther from forest edge and grid edge were settled earlier


a)
SINGLE BIRD
+ HU N = 52
● BG N = 81
DISTANCE TO FOREST EDGE (m)
SETTLEMENT DATE (Julian Day)
0
10
20
30
40
50
60
70
80
90
100
110
85
90
95
100
105
110
115
120
125
130

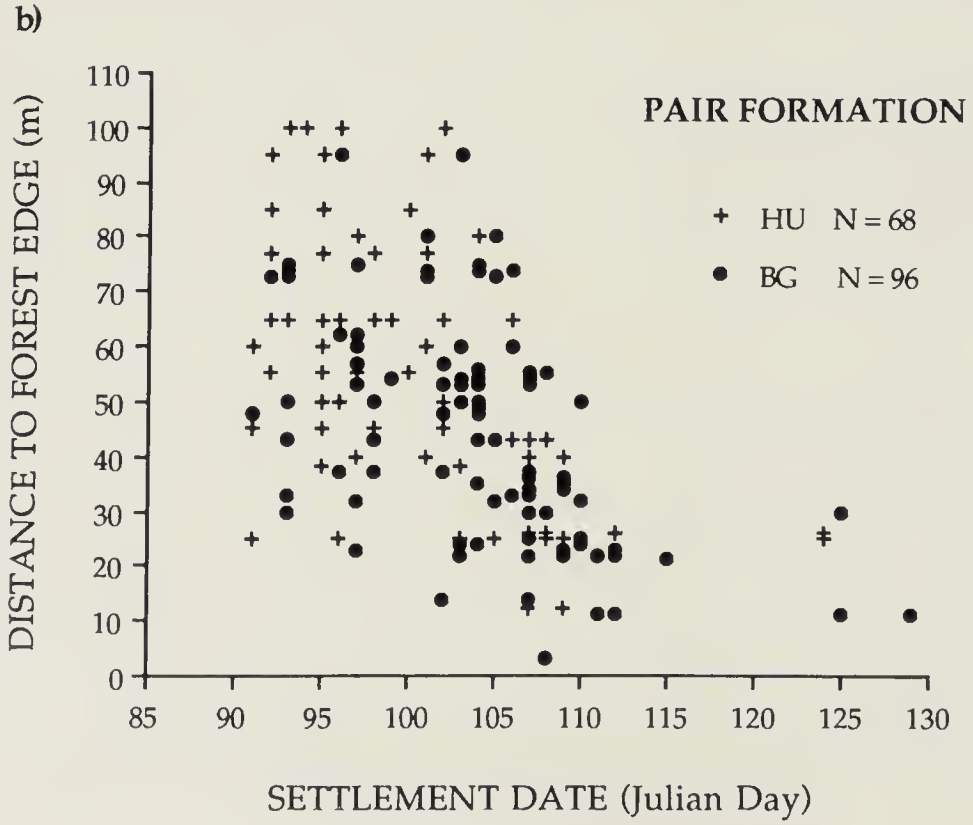

b)
PAIR FORMATION
+ HU N = 68
● BG N = 96
DISTANCE TO FOREST EDGE (m)
SETTLEMENT DATE (Julian Day)
0
10
20
30
40
50
60
70
80
90
100
110
85
90
95
100
105
110
115
120
125
130

TABLE 1

PEARSON CORRELATION COEFFICIENTS FOR SETTLEMENT DATES[a] OF TREE SWALLOWS WITH DISTANCE TO FOREST EDGE AND GRID EDGE AT BRIDGET'S GRID (BG) AND HUGHSON'S GRID (HU), 1986–1989

Grid	Years	Forest edge		Grid edge	
		One bird (N)	Pair (N)	One bird (N)	Pair (N)
BG	1986–1989	−0.538[b] (81)	−0.492[b] (96)	−0.469[b] (81)	−0.393[b] (96)
HU	1986–1989	−0.537[b] (52)	−0.548[b] (68)	−0.301[b] (52)	−0.263[b] (68)

[a] Julian day 91 = 1 April.
[b] Correlation coefficients are significant at $P \leq 0.05$.

by single birds and pair formation occurred earlier at these nest boxes in both grids. Distance to forest edge and to grid edge were significantly positively correlated with each other (at BG, 1986–1989, 0.82, $P < 0.01$; at HU, 1986–1989, 0.32, $P < 0.05$). Partial correlation analysis showed that nest-site settlement dates by Tree Swallows were negatively correlated with distance to forest edge at BG and HU (Fig. 3a, b), when controlling for distance to grid edge (Table 2). The alternative test (i.e., controlling for distance to forest edge) found no correlation of settlement date with distance to grid edge at either grid.

Early in the breeding season, many pairs of Tree Swallows initially defend territories that include more than one nest site (cf, Rendell and Robertson 1989). When a pair of Tree Swallows had a choice between nesting at one nest site or another, pairs chose most frequently to breed at the nest site farther from the forest edge. Tree Swallow pairs defended two or more nest sites on 44 occasions over four years (BG, 23; NB, 9; SP, 12). In 33 of these 44 cases, one or both nest sites were less than 30 m from forest edge (i.e., within the distance to edge where most House Wren and Eastern Bluebird pairs occupied nest sites; Fig. 2). In 25 of these 33 cases, Tree Swallows ultimately nested at the nest site farther from the forest edge (Binomial Test, $P = 0.002$). In these 25 cases, pairs were not forced to nest farther from edge as a result of losing a nest site to competitors but "chose" to breed at the nest sites farther from edge.

Predation and interference.—Predators preyed on nest contents, and House Wrens usurped focal nest boxes, at 43 of 299 (14.4%) breeding attempts (i.e., where at least one egg was laid) by Tree Swallows for all

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FIG. 3. Plots of settlement date (Julian day 91 = 1 April) at nest sites and distance to forest edge for Tree Swallows at Bridget's Grid and Hughson's Grid: (a) single birds, usually known to be males, 1987–1989, and (b) two birds (pair formation), 1986–1989.

TABLE 2

PARTIAL CORRELATIONS OF SETTLEMENT DATES AT BRIDGET'S GRID AND HUGHSON'S GRID, CONTROLLING FOR DISTANCE TO FOREST EDGE (FORED) AND GRID EDGE (GRDED), 1986–1989

Grid		Forest edge (controlling GRDED)		Grid edge (controlling FORED)	
		One bird (N)	Pair (N)	One bird (N)	Pair (N)
BG	settlement date	−0.304* (81)	−0.322* (96)	−0.066 (81)	0.024 (96)
HU	settlement date	−0.489* (52)	−0.507* (68)	−0.166 (52)	−0.110 (68)

* $P \leq 0.01$.

grids and years combined. The number of breeding attempts exceeds the number of nest sites occupied by Tree Swallows because several pairs renested in the same nest site in a given year (e.g., due to predation at first nest). Two terrestrial predators, raccoons (*Procyon lotor*) and black rat snakes (*Elaphe obsoleta*), were responsible for 62.8% (27/43) and 20.9% (9/43) of all acts of predation, respectively. House Wrens were responsible for the remaining 16.3% (7/43) of interference at Tree Swallow nests. House Wrens pecked eggs (cf, Belles-Isles and Picman 1986) and/or built their nests over active Tree Swallow nests. Predation by raccoons occurred only in 1987. Late in the breeding season of 1987, predator cones were installed at all boxes, effectively eliminating any threat of predation from terrestrial animals, but this did not prevent access to boxes by House Wrens. As a result, the following results describing predation by terrestrial animals are restricted to 1986–1987 only, while House Wren data from 1986–1989 are described.

From 1986–1987, 159 nest sites were available for use at all grids combined, and predation and/or interference occurred at 40 of these nest sites. The distribution of the number of nest sites where predation/interference occurred (presented as percentages in Fig. 4) relative to distance to forest edge did not differ from the distribution of nest sites where such events did not occur (Pearson chi-square, $\chi^2 = 2.67$, df = 5, $P = 0.75$). Therefore, predation and interference appears to have occurred at any nest site despite its proximity to forest edge. However, this analysis does not account for the different types of predators and competitors involved. Raccoons and black rat snakes were a threat to Tree Swallows at all distances from forest edge up to 80 m, but House Wrens interfered only at nests within 20 m of forest edge ($\bar{x} = 9.0 \pm 1.7$ m, range = 3.1–17.0 m, N = 7; including two acts of interference committed in 1988; Fig. 4). Clearly, the likelihood of a Tree Swallow nest being destroyed by House Wrens decreases as distance to forest edge increases.

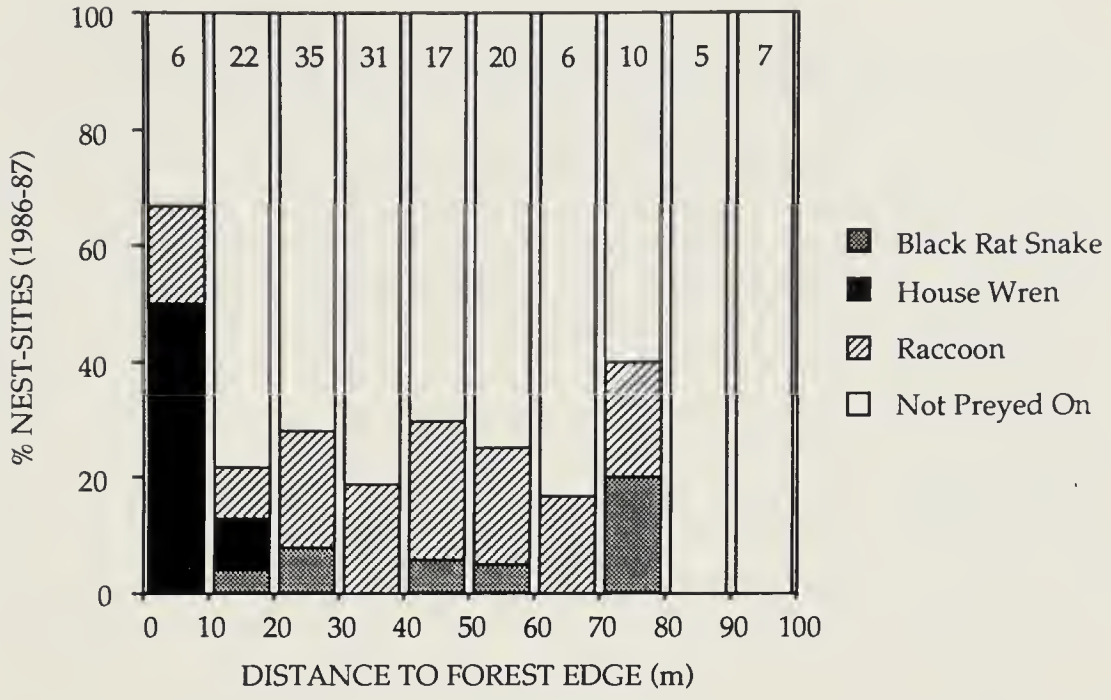

FIG. 4. Distribution of Tree Swallow nest sites that were usurped or where predation occurred, and those that were not influenced by predators or competitors, relative to distance to forest edge (1986–1987 for all predators and competitors). Sample sizes of the number of nest sites available for use are presented for each distance cell.

DISCUSSION

When Tree Swallows had a choice of nest sites on which to settle and breed, they avoided nesting close to forest edge. Single birds (assumed and often known to be early arriving males, Stutchbury and Robertson 1987a) settled at nest sites farther from forest edge first, and females subsequently settled first with males situated near the center of the population. Since Tree Swallows are limited by nest-site availability (Holroyd 1975, Stutchbury and Robertson 1987b, Rendell and Robertson 1989), rather than forego breeding, late-arriving birds were forced to use nest sites closer to forest edge. Apparently, both males and females selected nest sites based on the same criteria, consistent with the suggestion that characteristics of nest sites may act as cues to breeders concerning the likelihood of nesting success (Nilsson 1984, Finch 1989).

Our results appear to contradict Muldal et al. (1985) who studied spacing patterns of Tree Swallows in nest boxes arranged in spirals in the same fields as this study. One of their conclusions, that Tree Swallows settled at a spiral independently of its location in a field, was based on the assumption that settlement date is correlated with first egg date. Stutchbury and Robertson (1987a) have subsequently shown this not to be the case. Therefore, while their interpretation of patterns of actual nest-box

occupancy over short distances remains valid, the absence of direct information on settlement patterns prevented Muldal et al. (1985) from detecting preferences for nest sites in relation to location within a field.

Why should Tree Swallows avoid nesting close to forest edge? We suggest this behavior is a response to greater likelihood of interference by competing species, especially House Wrens, near forest edge. Similar to our study, Munro and Rounds (1985) found House Wrens typically nested within 30 m of forest edge, and Willner et al. (1983) found House Wrens nested in boxes closer to trees and shrubs than Tree Swallows, and that Eastern Bluebirds were intermediate to both species (see Fig. 2). Further, House Wrens commonly interfere with breeding attempts by Tree Swallows (Kendeigh 1941, D. M. Finch, pers. comm., this study), and Eastern Bluebirds, although not observed to usurp nest sites from Tree Swallows in this study, do compete aggressively for nest sites (Kuerzi 1941). Therefore, by selecting nest sites more distant from forest edge, Tree Swallows can avoid the costs of harassment or nest destruction which are incurred during competition with Eastern Bluebirds and House Wrens.

Tree Swallows may choose to nest farther from forest edge for other reasons as well. Tree Swallows are aerial insectivores that commonly forage over open fields and water. Nesting away from forest edge likely allows clear flight paths for foraging in the vicinity of the nest site. Also, some benefit may be derived from nesting centrally to other breeding pairs. For example, Tree Swallows respond to avian predators (e.g., Sharp-Shinned Hawk [*Accipiter striatus*]) by alarm-calling, mobbing, and chasing a threatening hawk. The characteristics of grid geometry (see Fig. 1; cf, Hamilton 1971, Wittenberger and Hunt 1985) may render birds nesting farther from forest edge, and/or centrally to other pairs, less susceptible to attacks from accipiters. Nesting centrally to other pairs may also reduce the likelihood of predation from terrestrial animals. However, our data on predation by raccoons and black rat snakes do not support this idea.

Many social and historical factors also play a role in nest-site selection. For example, the presence of a previous mate (R. R. Cohen, pers. comm.) or a history of successful nesting at a particular site (Pinkowski 1979, Sonerud 1985, Drilling and Thompson 1988) may influence where an individual Tree Swallow settles. In our study, all physical characteristics of nest sites (e.g., habitat structure, box height and orientation) were essentially uniform, except for distance to forest edge. Given the influence of social factors and past breeding experience on nest-site selection, it is remarkable that distance to forest edge apparently plays such an important role in determining nest-site selection and, hence, settling patterns of Tree Swallows.

Distance to forest edge is likely an important factor in nest-site selection

in natural habitats as well. In a study of Tree Swallows breeding at beaver ponds, Rendell and Robertson (1989) found nest cavities that were preyed on were considerably closer to shore (i.e., forest; $\bar{x} = 26.4 \pm 4.5$ m, N = 15) than those that fledged young (47.9 ± 9.2 m, 22), although this difference was not significant. Tree Swallows and other hole-nesters in these populations may increase their likelihood of reproductive success by choosing to occupy cavities as far from shore as possible upon returning each spring. Unfortunately, we do not have settlement data for Tree Swallows in natural populations.

In conclusion, when Tree Swallows had a choice of where to nest in a population, they chose nest sites farther away from forest edge. This behavior may be an adaptive response to a greater threat of competitive interference from other species for nest sites near forest edge. The addition of distance to forest edge to other characteristics of cavity nest sites that are known to influence reproductive success (i.e., cavity height, cavity volume) suggests that nest-site selection by secondary cavity-nesting birds is an important and complex decision involving many variables.

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DIURNAL TIME-ACTIVITY BUDGETS OF WINTERING CANVASBACKS IN LOUISIANA

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ABSTRACT.—We determined diurnal time-activity budgets of Canvasbacks (*Aythya valisineria*) at Catahoula Lake and at the Mississippi River Delta, Louisiana, from December 1987 to March 1988. Canvasback feeding, resting, locomotory, and comfort activities varied by month and location with a month-location interaction. Moreover, the percentage of time spent feeding varied by sex with a month-sex interaction. Study site differences in the time-activity budgets of wintering Canvasbacks may be related to characteristics of their foods, foraging mode, disturbance level, and physical features of habitats at the two study sites. Canvasbacks wintering in Louisiana generally spent less time feeding and more time resting during the day than they did in Mississippi or coastal South Carolina. Levels of agonistic behavior were lower than those observed in South Carolina. We found no evidence of male dominance of female Canvasbacks in Louisiana. *Received 14 Dec. 1989, accepted 22 Mar. 1990.*

Overwinter and annual survival probabilities of waterfowl may be influenced by their relative body condition in winter (Haramis et al. 1986, Hepp et al. 1986). Further, it has been suggested that waterfowl recruitment is correlated with winter body condition (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1986). Energy relationships between a bird and its habitat, as reflected in its body condition relative to other individuals, are mediated through the time-activity budget of the bird (Paulus 1988). Whereas many aspects of the behavior (Alexander and Hair 1979; Alexander 1980, 1987), nutritional ecology (Perry 1982, Perry et al. 1986, Lovvorn 1987), and population biology (Nichols and Haramis 1980a, b; Haramis et al. 1985) of Canvasbacks (*Aythya valisineria*) wintering in the Atlantic Flyway have been investigated, Canvasbacks wintering elsewhere, especially in the Gulf of Mexico region, have been inadequately studied. Louisiana is a major wintering area for Canvasbacks, providing habitat since 1985 for >25% of the continental population (U.S. Fish and Wildlife Service [USFWS], Office of Migratory Bird Management, unpubl. data). We report here on time-activity budgets of wintering Canvasbacks at two sites in Louisiana. Canvasback activities are compared among wintering populations and between the wintering and migration periods.

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STUDY AREAS AND METHODS

This study was conducted at Catahoula Lake (CL) in central Louisiana (31°15′N, 92°00′W) and at the Mississippi River Delta (MRD) in southeastern Louisiana (29°15′N, 89°15′W). These two sites were selected from nine that traditionally are used by wintering Canvasbacks because of their locations (inland vs coastal) and high use. Sixty-eight to 74% of all Canvasbacks observed on monthly statewide surveys in winter 1987–1988 were recorded on these two sites (D. W. Woolington, USFWS, unpubl. data). Maximum numbers of Canvasbacks censused were 58,000 on CL and 14,000 on the MRD.

CL is a large (12,150 ha), swallow basin in the Mississippi River floodplain. The lake is drained in the summer to stimulate plant growth and flooded in the fall to provide waterfowl habitat and hunting opportunity (Zwank et al. 1985). Local rainfall or flooding of the Mississippi River caused by major runoff events upstream may produce abrupt changes in lake levels. For example, in winter 1987–1988, lake levels increased 3.9 mm in four days following locally heavy rains. Water depth at the center of the lake ranged from 0.2 m to 5.5 m and averaged 3.1 ± 0.22 m ($\bar{x}$ ± SE) during the study.

The deltaic plain of the Mississippi River is a highly dynamic and complex wetland system (Bahr et al. 1983). Water levels in the marsh change daily and seasonally. Marsh flooding is directly influenced by tidal changes and stages of the Mississippi River. The Mississippi River exceeds flood stage about 25% of the year. River stage is generally highest in late winter and lowest in summer. High and low tides occur once each day with a maximum range of 0.3 m. Wind also exerts a major influence on water levels in the marsh. Onshore winds may impede river flow and cause back-flooding into the marsh, whereas sustained offshore winds tend to reduce marsh water levels.

Feeding sites used by Canvasbacks at the two study locations differed markedly from each other and from those used elsewhere by wintering Canvasbacks (e.g., San Francisco Bay, Chesapeake Bay, coastal North Carolina). At CL, open water feeding sites as deep as 6 m were used by Canvasbacks, but at the MRD, birds used deltaic splays (i.e., accreting mudflats receiving shallow, intermittent flooding) almost exclusively. Deltaic splays were pitted with shallow depressions generally <2 m in diameter. These depressions contained water even at low tide and presumably were the result of disturbance by grazing nutria (*Myocastor coypus*).

We observed Canvasback behavior at the two study sites during the first ten days of each month from December 1987 to March 1988. Our procedures generally followed those used on wintering and spring-staging Canvasbacks by Alexander (1980) and Lovvorn (1987). Three persons (two observers and one data recorder) conducted continuous observations from elevated platforms throughout the daylight period. Observations began with the random selection of a focal individual. The focal bird of a given sex was identified by selecting a random number (1–100) and counting that number of individuals of the same sex from the left to the right edge of the observation area (i.e., field of view including all birds for which sex and activity could be reliably determined). Once selected, the focal individual was observed for 5 min, during which instantaneous behavior was recorded at 15-sec intervals (20 observations per focal bird) (Weins et al. 1970). At the end of the 5-min observation period, another bird was chosen by selecting the fifth bird of the same sex to the right of the previous focal bird. If fewer than five birds were present in that field of view, then the first individual of the same sex in the next field of view to the right was chosen. When the entire observation area had been scanned, observations were resumed with the random selection of a bird as described above. Systematic scanning of Canvasback flocks, as outlined above, was followed to ensure that observations were obtained from throughout the observation area.

We categorized Canvasback activities as follows: *feeding*—behavior associated with food search (e.g., preparation for diving, diving and tipping-up), capture and handling; *resting*—inactive birds with head positioned low on chest, bill setting on breast, or sleeping with bill tucked into scapular feathers; *locomotion*—birds swimming or in flight; *comfort*—behavior associated with body maintenance; *alert*—bird vigilant, head held off shoulders but not performing any other activity; and *other*—behavior associated with courtship and mating, and agonistic behavior ranging from threats and avoidance to bill thrusts, chasing and fighting (Alexander 1980). Focal individuals flying outside the observation area were assumed to be in flight for the balance of the 5-min period, and observations were resumed at the start of the next period from the location where the bird took flight. Pairing status of the focal individual was assigned at the end of the 5-min observation period. Paired individuals were those showing active association; that is, copulation, mutual display, female tolerance of male, or nonrandom spacing. All agonistic displays within the field of view of the spotting scope were recorded (i.e., species and sex of participants, and outcome of interaction). Sex of all Canvasbacks in the observation area was determined at least once daily to calculate the ratio of males to females. Disturbances caused by human activities were noted.

We used a three-way analysis of variance including all interactions to assess the effects of sex, month, and study site on individual activities of wintering Canvasbacks (PROC GLM, Statistical Analysis System to perform calculations; SAS Institute, Inc. 1987). Because analyses of raw data and arcsine square-root transformed data ($p^{1/2}$) yielded similar results, we here report results based on raw data only. We used χ^2-tests to analyze agonistic behavior by sex and study site (Conover 1980). Expected encounter rates between sexes were derived from sex-ratio data.

RESULTS

Time-activity budgets of Canvasbacks at CL and the MRD were based on about 350 hours of behavioral observations made on 4245 focal individuals. All Canvasback activities varied by month and location with a month-location interaction ($P < 0.025$). Moreover, the percentage of time spent feeding varied by sex ($P = 0.0335$) with a month-sex interaction ($P = 0.0001$). Females fed more than males in early and late winter (Fig. 1). Except for feeding, however, activity patterns of male and female Canvasbacks were similar at both sites.

Canvasbacks at the MRD fed more than those at CL, especially in midwinter ($P < 0.0001$; Fig. 1). Resting was higher at CL than at the MRD in midwinter, but the reverse was true in December and March ($P < 0.0001$; Fig. 1). Time spent performing locomotory activities changed differently at the two study sites through the winter ($P < 0.0001$; Fig. 1). Canvasbacks swam more at CL than at the MRD in all months except January ($P \leq 0.0001$; Fig. 1). Time in flight averaged <1% at both study sites in winter 1987–1988. Comfort activities declined after December at both study sites, but were consistently higher at CL than at the MRD ($P \leq 0.0001$; Fig. 1).

Agonistic behavior was observed at both study sites in all months, but only in February did the percentage of time spent in intraspecific aggres-

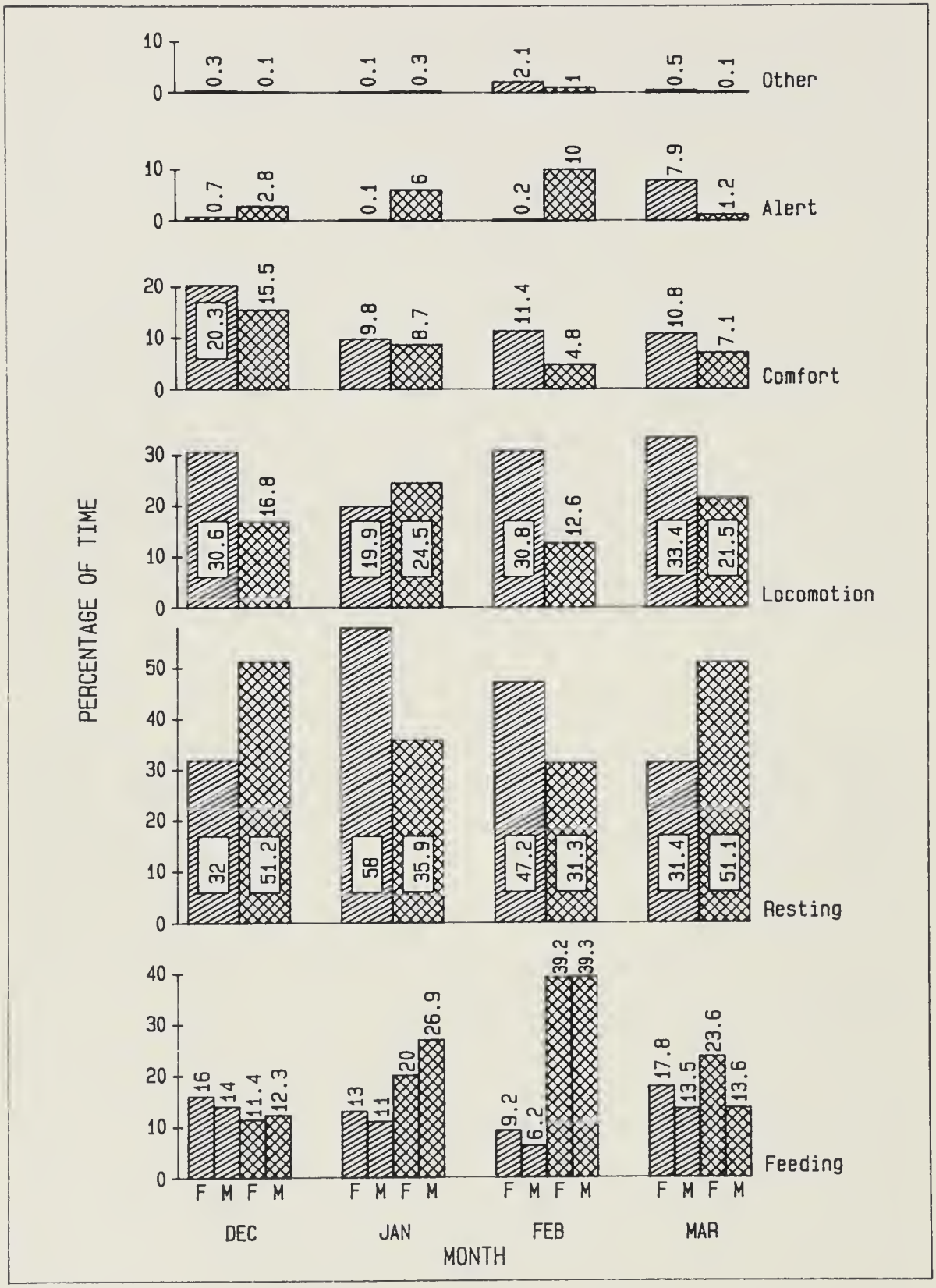

FIG. 1. Time-activity budgets of male (M) and female (F) Canvasbacks at Catahoula Lake (single-hatching) and the Mississippi River Delta (cross-hatching), Louisiana, in winter 1987–1988.

TABLE 1
DIURNAL TIME-ACTIVITY BUDGETS OF NONBREEDING CANVASBACKS

Period Location	Activity[a]				References
	Feeding	Resting	Movement	Comfort	
Fall-migrating					
Wisconsin	19	35	17	15	Takekawa (1987)
Wintering					
Mississippi	23	30	24	20	Christopher (1987)
South Carolina	33	34	20	11	Alexander (1980)
Louisiana					
Catahoula Lake	13	42	29	13	This study
Mississippi Delta	23	42	19	9	This study
Spring-migrating					
Wisconsin	39	22	8	13	Lovvorn (1987)
Ontario	36	17	14	15	Lovvorn (1987)

[a] Percentage of time spent performing activity.

sion exceed 0.5%. Levels of Canvasback aggression at the two study sites were similar, but patterns of aggression differed. Female-female aggression at the MRD was higher than predicted (N = 271 encounters; $\chi^2 = 13.6$; 3 df; $P < 0.005$). At CL, the occurrence of male-male interactions was low, and male initiation of aggression with females was higher than predicted (N = 125 encounters; $\chi^2 = 36.8$; 3 df; $P < 0.001$).

Interspecific aggression mostly involved American Coots (*Fulica americana*) associated with feeding Canvasbacks, and, to a lesser extent, Ruddy Ducks (*Oxyura jamaicensis*), Ring-necked Ducks (*Aythya collaris*), Northern Pintails (*Anas acuta*), American Wigeons (*Anas americana*), Gadwalls (*Anas strepera*), Green-winged Teals (*Anas crecca*), and grackles (*Quiscalus* spp.).

Courtship activities were rarely observed in wintering Canvasbacks in Louisiana. Pair bonding was evident in fewer than 1% of Canvasbacks observed in late winter.

DISCUSSION

Diurnal time-activity budgets of Canvasbacks vary seasonally and geographically (Table 1). We found that Canvasbacks wintering at CL and the MRD generally spent less diurnal time feeding and more time resting than did Canvasbacks wintering in Mississippi or coastal South Carolina (Table 1). Spring-migrating Canvasbacks fed more, but rested and moved less than wintering birds (Table 1). Time-activity budgets of wintering

Canvasbacks in Louisiana were most similar to those of fall-migrating birds (Takekawa 1987), but, because pauses occurring immediately before dives were classified as resting (vs feeding), time spent feeding probably was underestimated for fall-migrants (J. Y. Takekawa, USFWS, pers. comm.).

Study site differences in time-activity budgets of wintering Canvasbacks may be related to characteristics of their foods, foraging mode, disturbance levels, and physical features of habitats at the two sites. Diets of wintering Canvasbacks at CL and the MRD were similar in at least four respects: (1) they consisted of more than 97% plant material, (2) below-ground plant parts made up the largest portion (94 aggregate percent dry mass) of the diet, (3) dietary diversity was low, and (4) diet composition was independent of age, sex, or month (Hohman et al. 1990). Canvasbacks are behaviorally and morphologically specialized to feed on subterranean plant parts (Goodman and Fisher 1962, Tome and Wrubleski 1988). These foods contributed about 94% of the Canvasback diet both at CL and the MRD; however, the mode of foraging for below-ground foods differed between study sites. At the MRD, foraging birds were widely dispersed over mudflats (one bird per disturbed site) and fed in shallow water by tipping-up. In contrast, Canvasbacks at CL associated in large flocks and dived as deep as 6 m to obtain food.

Canvasbacks at the MRD seemed to forage around the perimeter of disturbed sites (i.e., enlarging disturbed sites), excavating with their feet and bill into previously undisturbed mudflats, where dry mass of subterranean plant parts was four-times greater than that within disturbed sites (Hohman et al. 1990). Aggressive defense of feeding sites was common at the MRD, as it was among diving ducks feeding on banana water-lily (*Nymphaea mexicana*) in coastal impoundments in South Carolina (Alexander 1980). Canvasbacks presumably do so because food resources at these sites are economically defensible. Habitat conditions favoring food resource defense by Canvasbacks at the MRD include shallow water depth, patchy distribution of food, considerable time and energy expenditures required to access food items, and large potential gain from foraging effort.

In winter, mudflats at the MRD are devoid of residual vegetation and are covered by a hardened crust. Disturbed sites may provide cues of food distribution and abundance to foraging Canvasbacks (indicating where foods may be found). Moreover, Canvasbacks feeding at the edge of disturbed sites avoided having to penetrate the sediment crust and thus may have foraged more efficiently than birds feeding in undisturbed areas. Although immature Herring Gulls (*Larus argentatus*) were observed harassing feeding Canvasbacks at the MRD (W. L. Hohman, pers. obs.), predation risks apparently are low and do not place individual foragers

at a disadvantage. Densities of subterranean plant foods at the MRD (Hohman et al., in press) and especially at CL (Wills 1965), may be high relative to those at other major Canvasback wintering areas, such as Chesapeake Bay (Orth and Moore 1981) and coastal North Carolina (Lovvorn 1987). Flock feeding probably was facilitated by the high density of chufa flatsedge (*Cyperus esculentus*) tubers at CL. Moreover, the economic feasibility of individuals defending feeding sites in water depths to 6 m was likely reduced.

Alexander (1980) observed high levels of aggression among Canvasbacks wintering in coastal South Carolina. Male Canvasbacks dominated females in aggressive encounters that occurred primarily among foraging birds (Alexander 1987). Nichols and Haramis (1980b) speculated that sexual segregation within flocks of wintering Canvasbacks (males being more centrally located within flocks than females) and sexual differences in migration patterns were the result of male dominance. We found little evidence of male dominance of female Canvasbacks in Louisiana. At CL, male aggression towards females was higher than predicted, but Canvasbacks at that location fed in large flocks, and aggressive encounters commonly occurred when a feeding (i.e., diving) bird resurfaced close to another bird, who became the aggressor. Because females fed more than males, they were more likely than males to be the target of aggression. Age also influences Canvasback dominance relationships (Alexander 1987) and might have contributed to an elevated level of female-female aggressive interactions at the MRD. Immature females were more numerous than immature males (W. L. Hohman pers. obs.), and probably required additional feeding time (relative to adults) to sustain a constant rate of fat deposition throughout the winter (Hohman unpubl. data). Thus they were likely to be involved in feeding aggression.

There were differences between study sites in the frequency of disturbance caused by human activities such as fishing, hunting, and commercial and recreational boating. Frequency of disturbance recorded during behavioral observations was higher at CL (N = 19 disturbances) than at the MRD (N = 9 disturbances), and this was reflected in increased time spent in locomotory and comfort activities at CL. Locomotory and comfort activities of Gadwalls, Mottled Ducks (*Anas fulvigula*), and Tufted Ducks (*Aythya fuligula*) also have been correlated with disturbance (Pedroli 1982; Paulus 1984a, b). Elevated levels of comfort activities recorded in December, especially preening, corresponded to completion of prealternate molt (Austin 1987, Lovvorn and Barzen 1988).

Diurnal time spent feeding varied by sex and study site. Alexander (1980) also found sexual differences in the diurnal time-activity budget of wintering Canvasbacks. Female Canvasbacks may be less efficient for-

agers than males (Takekawa 1987) and require more feeding time. At CL, females consistently spent more time feeding than males, but this was not the pattern in South Carolina (Alexander 1980) or at the MRD (this study). Diving ducks are known to shift from diurnal to nocturnal feeding in response to disturbance (Thornberg 1973, Pedroli 1982). Canvasbacks were known to feed nocturnally at both Louisiana study sites (about 25% of birds collected at night had food in their esophagi; W. L. Hohman, unpubl. data); however, the extent to which birds adjusted nocturnal activities to changes in daytime feeding is unknown.

Physical characteristics of wintering habitats, such as water depth (as affected by tidal cycle and river stage), exposure to wind and waves, and water and air temperature, potentially influenced Canvasback time-activity budgets at the two study sites. We attempted to control for weather factors by collecting behavioral observations from the two study sites simultaneously; however, CL observation areas were deeper, larger, more open, and further inland than those at the MRD. Physical conditions experienced by birds at CL probably were more severe than those at the MRD and may have contributed to study site differences in locomotory and resting activities. Tidal cycle (and river stage) probably influences Canvasback activity patterns at the MRD as it does other waterfowl wintering in coastal habitats (see Paulus 1988). Feeding seemed to be most intensive under low to intermediate tidal conditions, when water levels were shallow enough to permit tipping-up, but data collected here were inadequate to assess quantitatively the effect of tidal cycle (vs river stage) on Canvasback activities.

Activities of wintering Canvasbacks may influence their survival and subsequent reproductive performance. We suggest that the interval between departure from wintering grounds and arrival on areas used for nesting is a critical period for Canvasbacks. Canvasbacks defer pairing until spring migration (Weller 1965, this study); thus, in March and April they simultaneously incur energetic costs of both migration and courtship. Moreover, females initiate prebasic molt (Lovvorn and Barzen 1988) and energy/nutrient storage for reproduction before arrival on nesting areas (Barzen and Serie 1990). Energy reserves accumulated in late winter may be used to meet these costs. Birds at both study sites were fatter in late winter than in early winter, but Canvasbacks at CL were generally leaner than those collected at the MRD (W. L. Hohman, unpubl. data). The extent to which study site differences in Canvasback time-activity budgets influenced fat levels in birds at CL and the MRD, and the consequences of reduced fat levels on overwinter survival and subsequent reproductive performance of Canvasbacks wintering at CL, are still unknown.

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SONGS OF THE FOX SPARROW. III. ORDERING OF SONG

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ABSTRACT.—I studied organization of singing in Fox Sparrows (*Passerella iliaca*) breeding in northern Utah and southern Idaho during 1973 and 1974. Fox Sparrows possessed a variety of songs that, due to their uniformity in structure within and among individuals, could be categorized into five major types. Each song of an individual tended to be presented with equal frequency. Fox Sparrows presented their songs in particular sequences, singing each song once, until the entire repertoire was exhausted. The sequences in which individuals presented the songs in their repertoire did not change between successive utterances of a particular song, whether separated by singing sessions, days, or years. Markov chain analyses of the sequences of the songs accounted for the behavior of 53 of 56 birds by a first-order model, while the organization of singing of the remaining three birds was accounted for by a higher-order model. Neighboring territorial Fox Sparrows that shared similar song repertoires showed no preference for singing the same sequence of songs. Neighboring males which shared similar song-type repertoires showed no preference for sequencing their songs similarly. Matching of song-types among counter-singing neighbors did not occur and basically was precluded by each individual's rigid organization of singing. Functional and causal explanations for the style of singing in Fox Sparrows are discussed. The manner in which Fox Sparrows organize their singing suggests that the pattern of song presentation may simply crystallize at random during the first spring. *Received 21 Nov. 1989, accepted 10 Feb. 1990.*

There is great variation in the structure of primary song, size of the song repertoire and manner of sequencing songs in male passerines (Hartshorne 1973, Kroodsma 1982). Individuals of species characterized by one song-type generally do not vary the structure of song or, of course, the order of song presentation during singing. Individuals of species that tend toward large song-type repertoires are generally more variable. Some have songs that are structured similarly between individuals and the order of presentation is somewhat variable (e.g., Northern Cardinal [*Cardinalis cardinalis*] Lemon 1965, Lemon and Chatfield 1971), while others possess more individualistic song-types in which the structure of a major song-type may be considerably altered between successive utterances (e.g., Song Sparrow [*Melospiza melodia*] Mulligan 1966). In some species both styles may be used in different populations and the ordering of songs may be varied both within and among singing sessions. For a general review of the definition and use of song repertoires see Kroodsma (1982).

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Often as not, species with moderate-sized repertoires sing in bouts, wherein a single song-type is repeated a number of times prior to switching to a different type (eventual variety e.g., CCCCBBB . . .). Those species with large repertoires often sequence their songs in a more random manner, using "favorite" songs more frequently than others (more immediate variety e.g., LMQLLAMLZ . . .). There has been a concerted effort by researchers to fathom the significance of variation in repertoire size and the permutations of song ordering resulting in numerous functional (Whitney 1981, 1985; Catchpole 1982, 1989; Kroodsma 1982; Shy and Morton 1986; Stoddard et al. 1988) and causal (Hartshorne 1973, Lambrechts and Dhondt 1988) explanations. These studies have considered only those species which sing a single song repertoire or multi-song repertoire as described above.

Herein I describe the ordering of song-types during singing sessions in Fox Sparrows (*Passerella iliaca*). Fox Sparrows of North America are of interest because the structure and complexity of their song and the size of individual song repertoires in western races are intermediate in comparison with most other species and, in particular, with their close relatives in *Melospiza* and *Zonotrichia* (Martin 1977, 1979). It will be shown that the ordering of song presentation by Fox Sparrows is quite unlike that of their closest relatives and of emberizids in general. Particular attention will be paid to hypotheses that may explain the observed form of singing organization.

METHODS

Fox Sparrows in northern Utah and southern Idaho were recorded during the breeding seasons of 1973 and 1974 at 19 cm/sec on a Uher 4000 IC tape recorder equipped with a Uher 516 microphone mounted in a 60 cm parabolic reflector. Songs of all individuals were identified after their visual display on a Kay Electric Company Sona-graph (6061-B) at a wide band-pass setting. Although 153 males were recorded, only the 56 for which I had extensive data were analyzed in detail. Totals of 8, 15, and 7 males in 1973 and 9, 12, and 5 from 1974, with repertoires of two, three and four songs, respectively, were analyzed. Numerous recordings from more than 50% of the birds were gathered during singing sessions which occurred at various times of the day and various stages of the breeding season. Six individuals color marked in 1973 were also recorded in 1974. Because results indicated that individuals did not vary the frequency of occurrence of song-types sung between bouts, all recordings of an individual were pooled.

For all Markov chain analyses, the behavior of song presentation was considered to be stationary. This was assumed because the probabilities of events (song-types) at the beginning and at the end of behavioral sequences (singing bouts) were not significantly different at the $P > 0.05$ level in those sequences for which the entire bout was recorded. That is, no individual appeared to have a preferred song-type with which it began or terminated a bout of singing. Analysis of variance tests (Sokal and Rohlf 1969), with α at 0.05, were used to determine if the differences in the various parameters of song and singing were statistically significant.

Normal singing.—All analyses of the organization of singing in Fox Sparrows used recordings collected from territorial birds singing normally. The term "normal singing" (Hinde 1958:212) "signified singing when no recorded . . . conspecific . . . songs were played back . . . ." However, playback of conspecific songs may have been used prior to the recording session to elicit an individual's singing, or other conspecifics may have been singing within hearing range. Recordings were also used from singing sessions that were already in progress before I arrived and began recording.

The term "bouts" and "singing sessions" will be used interchangeably: both refer to the behavioral unit from the onset of singing until its termination, denoted by an interval of silence considerably longer than the mean interval between songs, which averaged 7.1 ± 2.9 [SD] (N = 29 birds and 725 inter-song intervals, at least 20 songs/bird).

Structure of song.—Fox Sparrow songs are composed of sequences of temporally discrete sounds, termed syllable-types, which may or may not be repeated within a song but by definition never occur in an abbreviated form. In all, I recognized 49 syllable-types (Martin 1977). Although the syllable-types and their sequences, which compose the introductory portions of songs, vary considerably among individuals, the terminal sequence of syllables of songs of many individuals tends to be similar. This structural similarity among renditions of song permits them to be categorized into one of five major song-types: A, B, C, D, and E (Table 1). Thus the main feature used to categorize songs as to their type, except song-type D, is the terminal flourish of syllable-types. Song-type D may be most easily characterized by syllable-types nearer the middle of the song (Martin 1977).

Because of the considerable variation in the syllable-type structure of the initial portion of individuals' particular song-types, those songs of individuals that are designated as being of the same major song-type are not generally identical in overall structure (Table 1). All five major song-types were represented by a large number of versions in which the introductory syllable-types and/or sequence varied among birds but the syllable-types and sequence of the ending among birds were nearly identical (Table 1). During 1973 and 1974, 13 versions were recorded for song-type A, 67 for B, 31 for C, 22 for D, and 13 for E. Distinguishing among song-types and song-versions is important in that many individuals (48 of 133) possessed more than one version of some major song-type, usually B or C. However, the overriding emphases should be on the fact that songs are easily classified to type and that a great percentage of birds have songs that are structurally very similar to each other (Table 1). Even birds with multiple versions of one particular song-type used their versions as functionally independent units during singing bouts. This emphasizes that the birds, as well as I, recognize and treat each of their renditions as discrete entities.

Units of analysis.—Fentress (1973:163) noted that ". . . the investigator of behavior is faced with a potential paradox in that categories of behavior must be formed . . . ," even though the categories may not be divisible or functionally independent, and that ". . . categories are necessary abstractions convenient for summarizing data and suggesting subsequent analysis." The syllable-types and sequences of syllable-types in particular song-types of individual Fox Sparrows were consistent between successive utterances, both seasonally and yearly (Martin 1977). The structure of each of the several songs of an individual, then, was rigidly determinisitic. Each song-type uttered by an individual, however, is likely to be followed by a different song-type and the ordering of different songs within bouts is nonrandom (Table 2). This latter phenomenon is easily visualized by observing portions of the raw field data of singing sessions, upon which some of these analyses are based, as shown in Table 3. Therefore, the units of behavior that were chosen for analysis of repertoire organization were the song-types presented by individuals during singing sessions. Recent work by Falls et al. (1988) presents data that support such an approach and categorization of vocal behavior. Their data indicate that in Western Meadowlarks (*Sturnella neglecta*)

TABLE 1

MOST COMMONLY SUNG SYLLABLE-TYPE SEQUENCES OF THOSE BIRDS WHICH POSSESSED A PARTICULAR SONG-TYPE IN 1973 AND 1974

Percent of birds possessing pattern				
1973	N	1974	N	Syllable-type sequence
				Song-type A
38	17	48	16	1, 2 or 3, 4, 5, 6, 7, 8, 9[a]
49	22	33	11	1, 2 or 3, 5, 6, 7, 8, 9
				Song-type B
38	24	28	15	1, 10, 17, 12, 22, 49, 25, 26, 27
25	16	16.6	9	1, 4, 14, 5 or 16, 20, 22, 49, 25, 26, 27
				Song-type C
39	27	31	20	1, 11, 34, 35, 29, 37, 38, (39)[b]
20	14	20	13	1, 36, 11, 28, 29, 37, 38, (39)
34	24	8	5	1, 3, 36, 11, 28, 29, 37, 38, (39)
				Song-type D
17	3	5	1	1, 10, 41, 42, 28, 24, 25, 49, 43
22	4	28	5	1, 10, 40, 41, 27, 28, 24, 25, 49, 43
				Song-type E
71	5	0		1, 3, 44, 31, 30, 45, 32, 25, 46
0		42	5	1, 2, 44, 17, 45, 32, 25, 26

[a] Syllable-types are designated numerically 1–49.

[b] Parentheses indicate syllable-types an individual may add or delete from its song between successive utterances. A complete list of the syllable-type sequences used may be found in Martin (1977).

those song-types long recognized by human observers are also the units recognized by the birds.

RESULTS

Frequencies of song-types within singing bouts.—Birds with repertoires containing two, three, and four songs tended to present each song with equal frequency (see Table 2). Aberrations (i.e., unequal frequencies of song presentation), however, were observed (e.g., see B32-73 and B62-74 in Table 3). Although there was no significant difference ($F = 2.16$, df $= 2, 27$, $P = 0.135$) in the percent of aberrations committed among birds with repertoires of two ($\bar{x} = 7.1 \pm 6.2$ [SD], N = 10), three ($\bar{x} = 12.6 \pm 13.7$, N = 10) and four ($\bar{x} = 17.4 \pm 12.0$, N = 10) songs; the trend was for those birds with larger repertoires to have a higher percentage of deviations in song ordering.

Ordering of song-types within singing bouts.—The sequences of song presentation of individual Fox Sparrows were analyzed to determine the

TABLE 2

REPRESENTATIVE FIRST- AND SECOND-ORDER MATRICES OF THE FREQUENCIES OF TRANSITIONS BETWEEN SONGS IN FOX SPARROWS WITH REPERTOIRES OF TWO, THREE AND FOUR SONGS

EXAMPLE

		To song																	
					B28-74-BC			B29-73-BC			B21-74-BCC′				B4-73			
		A	B		B	C		B	C		B	C	C′[a]		B′	A	C	B
From	A	0	11	B	6	32	B	0	66	BB	0	0	0	B′B′	0	0	0	0
song	B	10	0	C	41	0	C	66	0	BC	0	0	65	B′A	0	0	31	0
										BC′	2	0	0	B′C	0	4	0	0
										CB	0	0	0	B′B	1	0	0	0
										CC	0	0	0	AB′	0	0	0	0
										CC′	66	0	1	AA	0	0	0	0
										C′B	0	67	2	AC	0	0	0	0
										C′C	0	0	0	AB	3	0	0	0
										C′C′	1	0	0	CB′	0	0	0	0
														CA	0	0	1	3
														CC	0	0	0	0
														CB	32	0	0	0
														BB′	0	32	4	0
														BA	0	0	0	0
														BC	0	0	0	0
														BB	0	0	0	0

	B62-74-BCB′ or A			B21-75-BCC′				B4-73-B′ACB				
	A	B	C		B	C	C′		B′	A	C	B
A	12	2	12	B	0	69	2	B′	0	34	4	1
B	10	0	16	C	0	0	68	A	0	0	33	3
C	6	24	3	C′	69	0	1	C	0	4	0	34
								B	38	0	0	0

[a] An apostrophe indicates a multiple version of song-type.

TABLE 3
SEQUENCES OF SONGS SUNG BY INDIVIDUAL FOX SPARROWS

Bird	Sequence of songs
B4-73-ACBB′[a]	ACBB′ACBB′ACBB′ACBB′AC//=[b]BB′ACBB′ACBB′A//CBB′ACB// B′BB′AC[c]BB′ACBB′ABCB′B′ACBB′AC//BB′ACBB′ACBB′ACBB′A
B15-74-ACB	BACBACBACBACBACBACBACBACBAA// ACBABACBCBACBACB//CB//CBAACBA//ACBABACB// CBACBACBACBACCA//CBACBA//AACBACB
B32-73-BDC	CDBDCBDCBDCBDCBDCBDCDBCBDCBDCBCCBDCBDCB-DCBDCBDCBDCBDCBDCBDCB//CB// BDCBDCBDCBDCBDCBDCBDCBDC//CBDCBCC// BBDCBDCBDCB//DCBDCB
B62-74-BCB′ or A	BCB′ACCABCB′ACAACBAAA// CBCB′CBCB′ACBCABAACBCB′CBACABACBCB′// CBCB′CCBCB′ACAAACBACBCCBCB′C
B9-73-BC	BCB//CBCBCBCBCBCBCBCBCBCBCBCBCBCBCBCBCB-CBCBCBC
B26-74-ABC	ABCBC//CABCABCABCBCABCABCBCAB-CABCBCABCBCABCBCBCABCBC// CABCABCBCABCBCABCBC// BCABCBCABCBCABCABCABCBCABCABCBC

[a] An apostrophe indicates a multiple version of a song-type within a repertoire.
[b] // Denotes end of one singing bout and the start of another; this separation may span minutes, days, or, as in B4-73, B15-74 and B9-73, years.
[c] Underlined passages indicate areas where preferred order was lost and quickly regained.

appropriate order of Markov chain model (if there was one) that could predict the observed data using the sequential test of Anderson and Goodman (1957). These analyses are comparable to those used by Lemon and Chatfield (1971, 1973) to investigate the organization of singing in birds.

Markov chain models are distinguished by the concept of order. If the order is zero, knowledge of past events (song-types) provides no information in predicting the current event. If the order of the Markov chain is one, knowledge of the immediately preceding event provides the information for predicting the current event, but information prior to the preceding event does not provide information for a statistically better prediction.

The procedure to find a Markov chain (of some order) that best describes the observed sequences of events (according to Anderson and Goodman 1957), is test H: $u = r$ versus H_A: $u = r + 1$, where r is the order of the Markov chain. The test procedure is sequential in nature. Testing begins with the comparison of H: $u = O$ with H_A: $u = 1$ by using the data of

events to compute a test statistic T. If T is less than the specified critical value, t^* ($* = P = 0.05$), then H is accepted; otherwise, H_A is accepted. As long as H_A continues to be accepted, further tests of higher orders are continued by increasing the order of r by one and performing the subsequent comparisons. The sequence of tests is concluded when at some point H is accepted. The level at which H (r of H) is accepted defines that level (order) which is appropriate for accounting for the ordering of the data (i.e., knowledge of the r order preceding event provides a better statistical basis for predicting the current event than a model that denies knowledge of the r order preceding event). Thus, the H that is finally accepted indicates the order of Markov chain model which best accounts for the ordering of the observed data. More detailed examples are presented by Anderson and Goodman (1957), Lemon and Chatfield (1971, 1973) and Cane (1978).

My analyses demonstrated that the sequencing of presentation in 17 birds with two song repertoires followed a first-order Markovian model (Table 4). A first-order Markov chain model was also accepted as predicting the sequencing of songs in 36 of 39 birds with repertoires of three or more songs (Table 4).

On the basis of these analyses both zero- and first-order hypotheses were rejected for three birds that possessed repertoires of three or more songs. Insufficient length of song sequences for these three individuals prohibited testing between second- and third-order models of the birds' sequences of songs which could be better accounted for by a higher-order model. Table 4 lists the T values for all tests performed.

Preference for particular song orders.—Birds banded in 1973 that returned to breed in 1974 ordered their songs in the same sequences (B4-73, B15-74, and B9-73 in Table 3), or when they initially deviated from their preferred song order they rapidly regained their preferred sequence (see B4-73 and B15-74 in Table 3). A few individuals with repertoires of three songs alternated between singing a three song sequence and a five song sequence (see B26-74 and B62-74 in Table 3). There was little correlation between the song-type repertoires of neighboring Fox Sparrows (Martin 1976, 1977).

Twelve of the 30 birds in 1973 and four of the 26 birds in 1974 possessed two versions of a single song-type. Nine birds sang multiple versions of song-type C and seven sang multiple versions of B. Of these 16 birds, seven had repertoires of only three songs. Thus, their multiple versions of either B or C were presented sequentially (see B21-74, Table 2). In those remaining nine birds possessing a repertoire of more than three song-types, the preferred sequence of song presentation of five individuals coupled versions of a song-type together (e.g., B4-73-BACB, Table 2).

TABLE 4

VALUES OF *T*-STATISTIC FOR FIRST- AND SECOND-ORDER MARKOV CHAIN ANALYSES

Bird	*T* value for		df for	
	1st order	2nd order	1st order	2nd order
B5-74	240.32	12.03	4	12
B6-74	132.00	8.5	9	36
B7-74*	162.46	40.6*	9	36
B9-74	616.24	10.67	9	36
B13-74	17.67	1.14	1	2
B14-74	39.09	1.00	1	2
B15-74	26.87	2.00	1	2
B16-74	18.33	3.81	4	12
B19-74	164.55	4.10	4	12
B21-74	430.48	0.08	4	12
B22-74	571.08	15.87	4	12
B26-74	182.16	0.85	4	12
B28-74	86.92	1.52	1	2
B29-74	281.33	0.0	4	12
B30-74	66.83	0.18	4	12
B31-74	226.02	15.98	4	12
B35-74*	32.89	30.66*	4	12
B36-74	28.80	0.18	1	2
B39-74	94.80	13.31	9	36
B47-74	23.23	1.65	1	2
B51-74	263.36	0.0	9	36
B55-74	17.09	0.20	1	2
B58-74	13.40	0.617	1	2
B59-74	364.46	3.50	4	12
B60-74	54.0	0.0	9	2
B62-74	54.17	13.86	4	12
B1-73	166.42	6.6	4	12
B3-73	32.28	0.98	1	2
B4-73	337.54	40.85	9	36
B5-73	97.85	65.70*	9	36
B6-73	137.39	2.57	4	12
B8-73	83.20	3.82	4	12
B9-73	74.86	0.0	1	2
B14-73	188.45	1.47	9	36
B15-73	264.16	19.80	4	12
B18-73	59.66	0.27	1	2
B21-73	138.76	20.04	4	12
B24-73	40.98	16.5	4	12
B25-73	45.52	20.18	4	12
B29-73	182.99	0.0	1	2
B30-73	116.96	2.1	4	12
B32-73	124.77	0.0	1	2
B34-73	188.45	17.69	9	36

TABLE 4
CONTINUED

Bird	*T* value for		df for	
	1st order	2nd order	1st order	2nd order
B35-73	114.22	25.36	9	36
B37-73	195.10	13.32	9	36
B38-73	254.66	0.0	4	12
B41-73	76.83	0.0	4	12
B44-73	68.93	0.07	4	12
B53-73	58.54	1.63	1	2
B54-73	68.91	0.62	1	2
B55-73	129.80	14.27	4	12
B57-73	122.67	16.77	4	12
B63-73	227.22	14.24	4	12
B65-73	108.03	23.95	9	36
B66-73	98.02	4.95	4	12

First-order df = $(m - 1)^2$ and second-order df = $(m)(m - 1)^2$. An asterisk indicates those second-order values which are significant at $\alpha = 0.05$.

Cadence of song presentation during singing bouts.—Cadence of singing (length of intersong intervals) in those birds that had repertoires of two ($\bar{x} = 6.3 \pm 2.3$, N = 9), three ($\bar{x} = 7.3 \pm 3.1$, N = 10) and four ($\bar{x} = 7.5 \pm 3.2$, N = 10) songs was not significantly different ($F = 0.412$, df = 2, 27, N = 29). Most singing bouts ended abruptly and there was little consistent variation in the cadence of song presentation between the first and last halves of singing sessions. At times the silent interval between the terminal two or three songs of a singing session was noticeably longer than normal but this phenomenon was rare and did not occur consistently in any particular individual. Two conditions with which aberrant timing did appear to be associated, however, were: (1) long singing sessions, provoked by repetitive playback, and (2) the termination of breeding activities in mid-July. Either of these conditions could have resulted from frustration or decreased motivation to sing arising from the performer's failure to locate the intruding conspecific (simulated by playback) or from decreased hormonally induced impetus to sing, respectively.

DISCUSSION

These data clearly show Fox Sparrows rigidly order the sequence of their songs during bouts of singing and they sing with immediate variety (Hartshorne 1973), singing each of their songs once until all songs in their repertoire have been presented (Tables 2 and 3). Such a system of ordering

is best described by a first-order Markov model (Table 4). Further, the order of song sequencing of an individual does not appear to change through time (Table 3). This method of ordering song is atypical of virtually all passerines (Hartshorne 1973, Kroodsma 1982), except possibly for the Large-footed Finch (*Pezopetes capitalis*) of Costa Rica (D. E. Kroodsma pers. comm.).

Fox Sparrows with multiple versions of a song-type do not appear predisposed to order their songs so that versions are separated by one or more songs of a different type (Tables 2 and 3). Such ordering of song is also quite unlike that observed in other passerines. In species that possess multi-song repertoires, songs that are more similar in structure tend to be grouped into long bouts of near identical songs or ordered in a fairly random manner whereby similar songs are interspersed among dissimilar types (Verner 1975, Kroodsma and Verner 1987, Kroodsma 1982, Lambrechts and Dhondt 1988). Comparison of syllable-type sequences of songs listed in Martin (1977 and unpubl.) indicate that, based upon shared syllables, song versions of a particular song-type are indeed more similar to each other than they are to songs of a different type. Further, playback experiments by Martin (1980) indicate that male Fox Sparrows treat different songs as equivalents.

The style of singing of Fox Sparrows immediately raises two questions: (1) Why do Fox Sparrows possess a repertoire of songs which appear to be identical in function and, therefore, why are they redundant in their singing? and (2) Why do Fox Sparrows order their song-types so precisely during singing bouts?

Redundancy in singing.—Investigators seeking a functional explanation for the existence of repertoires and redundancy in singing have proposed that such behavior may be selected for by pressures of intersexual and/or intrasexual selection and/or individual recognition (see Dawson 1982, Kroodsma 1982). Studies seeking a causal explanation for redundancy in repertoires have proposed hypotheses focusing on physiological exhaustion of the song-producing mechanism (Lambrechts and Dhondt 1988) or habituation processes affecting (either or both) the singer or listener (see Kroodsma 1982) promoted by non-versatility in singing (Hartshorne 1956, 1973) or some form of neurological facilatory/inhibitory feedback mechanism (Todt 1975, Whitney 1985).

Redundancy is important functionally for decreasing the probability that receivers will miss or "misinterpret" the signals broadcast (Peek 1972a, b) and when there are relationships among individuals which may vary through time (Wilson 1975:200). Frequently repeated signals allow individuals to reassess their relationships, such as fluctuating territory

boundaries (Stenger and Falls 1959). Presumably, redundancy in Fox Sparrow singing has the same functions.

Redundancy, as measured by the total number of songs sung per unit time, also appears important in mate attraction. Regardless of repertoire size, the number of songs sung per unit time is much greater while a male is actively attempting to attract a mate (e.g., Catchpole 1973, Nolan 1978). Male and/or territory quality appears to be positively correlated with the total amount of time spent in song (Møller 1983) or the length of song (Lambrechts and Dhondt 1986). Pied-flycatcher (*Ficedula hypoleuca,* Gottlander 1987) and Willow Warbler (*Phylloscopus trochilus,* Radesater et al. 1987) females select first (prefer?) males singing with the most rapid song rate. The manner in which Fox Sparrows apportion time singing throughout the breeding season (Martin 1979) matches these intra- and intersexual functional explanations for redundancy in song.

Why individual Fox Sparrows sing more than one major song-type and order these so rigidly within singing sessions cannot be answered as easily. In some species with numerous song-types, counter-singing rivals tend to match each other's songs with similar song themes. Such counter-singing may allow for numerous responses (thus, stronger defense) between territorial males (Krebs et al. 1981). Matching of song themes by neighbors may also facilitate neighbor-neighbor recognition (Kroodsma 1976), whereas switching from one song-type to another during counter-singing may enable rivals to retaliate with more forceful threats (Dixon 1969). Thus, matching serves as a graded signal indicating level of aggressive intent (Krebs et al. 1981, Todt 1981, Shy and Morton 1986). Possession of multiple song-types and matched counter-singing have the potential also to convey information about local population density (Krebs 1977, Yasukawa 1981) and the distance between songsters (Morton 1982). McGregor and Krebs (1984) have indicated that birds may range a particular song-type even if they do not possess such a theme in their repertoire, but are familiar with the song-type from the singing of their neighbor. The structure of Fox Sparrow song appears well-designed for encoding individual and population identity (Martin 1977, 1979) and ranging is conceivable based upon shared song units. In 1973 and 1974, 99% and 92%, respectively, of all birds possessed one version of song-type C and there was great sharing of syllable-types and notes among birds (Martin 1977, 1979). Thus, as birds rapidly cycle through their repertoire during counter-singing, the probability is great that they hear both familiar and shared song units.

Such functions, however, do not appear to be the primary objectives of the organization of singing in Fox Sparrows. Matched counter-singing

among rivals is essentially precluded by the rigid ordering of each individual's songs and non-sharing of similar major song-types or size of song repertoire. Interestingly, recent playback experiments have shown that matched counter-singing and increased aggressive intent is not common to all species in which individuals have repertoires of shared song-types. The Wood Thrush *Hylocichla mustelina* (Whitney and Miller 1983) and, most interestingly, the close relative of the Fox Sparrow, the Song Sparrow (McArthur 1986), appear to demonstrate aggressive responses that are inversely related to the closeness of the match between a playback song and one in the test bird's repertoire.

Preliminary playback experiments broadcasting different size song repertoires to male Fox Sparrows indicate that they probably do not habituate less rapidly to larger repertoires (Martin, unpubl. data). In this respect, Fox Sparrows behave similarly to Sedge Warblers (*Acrocephalus schoenobaenus*) (Catchpole 1989) and Song Sparrows (Lemon et al. 1981). In Song Sparrows, the rate of switching between song-types is positively correlated with the intensity of agonistic stimulation and versatility functions both as a stimulus and a response (Kramer et al. 1985). The individual performing the behavior along with its listeners is thus central to any consideration of habituation or potential for what Kramer and Lemon (1983) hypothesize as motivational communication.

The most parsimonious functional explanation for the ordering of songs in Fox Sparrows, therefore, may well be that the increased variety it produces decreases habituation in the singer, allowing for increased song production, which is more stimulatory to the female (Kroodsma 1976) and is also a most effective agonistic signal to males (Kramer et al. 1985). Male Western Meadowlarks (*Sturnella neglecta*) switch song-types at a greater rate during mate attraction (Horn 1987). Recent comparative review by Catchpole and McGregor (1985) of sexual selection pressures and song complexity in birds in the genus *Emberiza,* in the same subfamily as Fox Sparrows, supports the contention that song versatility in monogamous buntings is strongly positively correlated with intersexual selection for male quality (Catchpole and McGregor 1985). Further, high rates of song-types switching in Song Sparrows appears indicative of greater annual and lifetime reproductive success. Males with larger repertoires and, most importantly, larger half-hour repertoires, had higher fitness values and longer territory tenure (Hiebert et al. 1989). Larger half-hour repertoires are the product of rapid song-type switching, a phenomenon that within the complex of *Zonotrichia-Melospiza-Passerella* is taken to its extreme by Fox Sparrows. Taken together, the correlations between Fox Sparrow singing behavior and that of other species indicates it may

have been influenced more by intersexual selection pressures rather than intrasexual pressures.

Ontogeny of song ordering.—The view that versatility in performance decreases either neurological and/or physiological habituation and/or exhaustion has met with agreement in the writings of Hinde (1958), Kroodsma (1982), Whitney (1981, 1985), and Lambrechts and Dhondt (1988). The question remains, however, as to how Fox Sparrows come to sing the order of songs that they do. If the bird has learned three song-types (e.g., A, B, and C), then two possible methods of singing to avoid habituation/exhaustion would be to alternate perfectly among song-types or alternate randomly between song-types. Depending upon the decay value of the song and/or the time-scale of the perception of the bird, either one of these two methods may be selected. Such behavior, however, would not negate an individual's changing the order of song-types between singing bouts, or even within bouts, once an aberration in ordering had been made (see Falls and Krebs 1975). In Fox Sparrows, the retention of particular sequences of song-types between singing bouts, even those separated by days or years, and the rapid compensation of their deviations in ordering during singing sessions (Table 3), suggests that antihabituation/exhaustion pressures, if present, are not the only factors contributing to the unique organization of their singing.

The fact that the sequencing of songs by Fox Sparrows is constant through time requires that one or more additional factors, coupled with habituation/exhaustion avoidance, must be affecting the behavior. Choices for additional effectors appear to be only three. First, rigid ordering could be achieved by the probability that the effects of the several song-types are graded, such that A is always highest and C least. Such gradation should lead to the phenomenon of many singing bouts of an individual beginning and possibly ending with particular song-types. However, as already discussed, this is not the case (Table 3). Those birds with multiple versions of a song-type did not appear to space the occurrence of song-type versions in any specific manner. Two versions of a song-type were as likely to be presented sequentially as not.

Second, rigid ordering could be attained through a system in which all song-types are of equal valence, and an individual learns a particular sequence of song presentation from conspecifics early in life or from neighbors while settling on territory. Acquisition of specific song structure occurs within the first 90 days of life in laboratory-reared White-crowned Sparrows (*Zonotrichia leucophrys*) (Marler and Tamura 1964) and a sensitive period of song learning is most pronounced between three and 10 weeks of age in Song Sparrows (Mulligan 1966, Marler and Peters 1987)

and Swamp Sparrows (*Melospiza georgiana*) (Kroodsma pers. comm., Marler and Peters 1982). Further sequence of song presentation is learned in at least one passerine, the Long-billed Marsh Wren (*Telmatodytes palustris*) (D. E. Kroodsma pers. comm.). Payne (1981, Payne et al. 1981) has shown learning of song during the first spring occurs in Indigo Buntings. Young Fox Sparrows fledge by early June but remain associated with their parents upon the breeding territory until the fall migration; adult males continue to sing until mid-July. Immature Fox Sparrows, thus, have an extended period in which they may learn syllable-types, song-types, and a sequence of song ordering.

Third, a pattern of song ordering may simply crystallize during subsong in a manner similar to song crystallization from subsong during the first spring. Individuals then would follow a prescribed order, regardless of where within the sequence of songs singing began. If either the second or third hypothesis is functioning then the initial song of a sequence could be randomly determined, as observed in the organization of singing by Fox Sparrows. Although the last two hypotheses are both plausible, the culturally transmitted song-sequence model seems unlikely. Such a model would probably result in neighborhood or populational "song-sequence dialects" similar to the song-structure dialects found in many *Zonotrichia* and *Melospiza* sparrows. Dialects consisting of one or a few preferred song-sequences clearly do not occur in Fox Saprrows. Thus, a model of random song-sequence crystallization seems most applicable.

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BEHAVIOR, BODY CONDITION, AND FOODS OF BUFFLEHEADS AND LESSER SCAUPS DURING SPRING MIGRATION THROUGH THE KLAMATH BASIN, CALIFORNIA

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ABSTRACT.—Behavior, body condition, and food habits of Buffleheads (*Bucephala albeola*) and Lesser Scaups (*Aythya affinis*) were studied in the Klamath Basin in northern California in spring 1986 and 1987. Peak Lesser Scaup and Bufflehead numbers were present in early February and mid-March, respectively. The first spring migrants of both species were mostly paired or courting adults. Buffleheads and Lesser Scaups spent 63–82% and 23–50% of their diurnal activities feeding, respectively. Both species consumed primarily (66–77% volume, 58–72% dry weight) invertebrates. Chironomidae larvae were the most important food consumed by both species. Body and carcass masses of both species were near mid-winter levels but below masses observed upon their arrival at northern breeding areas. Our data indicate that wetland habitats in the Klamath Basin provide important food and resting resources for migrating Buffleheads and Lesser Scaups. *Received 11 Sept. 1989, accepted 20 Mar. 1990.*

The biology of diving ducks (tribes Aythyini and Mergini) during spring migration is poorly documented. For some waterfowl species, habitat conditions on wintering and spring migration areas influence their ability to obtain nutrients required to meet the nutritional costs of migration, courtship, pairing, and molt (e.g., Heitmeyer 1988). Additionally, lipid and protein reserves stored during late winter and spring may influence the reproductive potential of Lesser Snow Geese (*Chen caerulescens*) (Ankney and MacInnes 1978, Wypkema and Ankney 1979, Davies and Cooke 1983), Canada Geese (*Branta canadensis*) (Raveling 1979), and Mallards (*Anas platyrhynchos*) (Krapu 1981, Heitmeyer 1988, LaGrange and Dinsmore 1988). In contrast, nutrient storage patterns of diving ducks are less well-known (but see Hohman et al. 1988).

The Klamath Basin in southern Oregon and northern California is a primary migration area used by many waterfowl in the Pacific Flyway, including Buffleheads (*Bucephala albeola*) and Lesser Scaups (*Aythya affinis*) migrating along intermountain corridors to breeding areas in western North America (Erskine 1972, Bellrose 1980). We collected data on habitat use, behavior, body condition, and food habits for Buffleheads and Lesser Scaups during spring migration through the Klamath Basin. These

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data help describe the behavioral and physiological ecology of these species, and the importance of resources provided at this important migration stopover area.

STUDY AREA AND METHODS

Data were collected at Lower Klamath National Wildlife Refuge (LKNWR) located along the California-Oregon border. LKNWR contains 20,944 ha of shallow palustrine wetlands, grasslands, and croplands. Wetlands are managed primarily as permanently (PF) and seasonally flooded (SF) marshes. PF marshes are mostly 1–2 m deep and dominated by cattail (*Typha* spp.); hardstem "tule" bulrush (*Scirpus acutus*); many "moist-soil" species including alkali bulrush (*Scirpus robustus*), smartweeds (*Polygonum* spp.), common barnyard grass (*Echinochloa* spp.), dock (*Rumex* spp.), and various sedges; and sago pondweed (*Potamogeton pectinatus*). SF marshes are typically flooded <1 m deep from early fall (August–September) through spring (April–May) and are dominated by smartweeds, common barnyard grass, dock, sedges, foxtail (*Hordeum fueginus*), and goosefoot (*Chenopodium* spp.). Wetlands at LKNWR are approximately 45% SF and 55% PF. Other habitats on LKNWR include barley fields, grazed and ungrazed uplands, and vernal pools dominated by flixweed (*Descurainia sophia*) and saltgrass (*Distichlis spicata*). Rainfall in the Klamath Basin averages 15 cm during September–March and was near long-term means in 1985–1986 and 1986–1987 (U.S. Department of Commerce 1985–1987). Temperatures in the Klamath average 5°C and 7°C during February and March, respectively, and were near long-term means during this study.

Bufflehead and Lesser Scaup numbers on LKNWR from September through April 1985–1986 and 1986–1987 were estimated during aerial surveys conducted by LKNWR personnel. We observed and collected birds on LKNWR during 8–18 March 1986 and 24 February–18 March 1987.

We observed flocks during all daylight hours and recorded their activity using scan-sampling techniques (Altmann 1974). Scans were made in both PF and SF habitats selected opportunistically; both species were present in all but three scans. We repeatedly scanned a selected flock for at least 20 min. A total of 22.8 h of time-activity data, consisting of 172 scans was collected. Numbers of Buffleheads and Lesser Scaups observed per scan averaged 61 and 71, respectively. We recorded bird activity as follows: (1) feeding (included picking at foods on the surface, diving, and dive pauses); (2) resting (sleeping and loafing); (3) preening (also includes drinking and bathing); (4) locomotor (swimming and flight); (5) courtship (courtship displays, courtship flights, and copulations); and (6) agonistic (alert posture, intra- and inter-specific aggression). Determination of courtship displays followed Myres (1959), Johnsgard (1965), and Erskine (1972). Scan-sampling underestimates time spent feeding by diving ducks since birds cannot be observed while under water (Hohman 1984, Baldassarre et al. 1988). Although we scanned flocks at a slow rate in an effort to reduce this bias, our behavior data undoubtedly underestimate time spent feeding.

We used plumage characteristics (Palmer 1976) to determine sex ratios. A higher percentage of Buffleheads than recorded may have been male because females and immature males have similar plumage. Most juvenile Buffleheads migrate several weeks later in spring than adults (Erskine 1972). Therefore, our observations in early spring migration were likely only slightly biased toward females. Prior to or following each set of scans, we determined the pairing status (paired or unpaired) of female Buffleheads and Lesser Scaups from displays and association of the female with a male (Johnsgard 1965).

Buffleheads and Lesser Scaups were shot in both SF and PF habitats. Immediately following collection, the esophagus and proventriculus of each bird was removed and stored

in 95% ethanol for subsequent analyses of food habits. We sorted and identified contents of the esophagus and proventriculus within six months of collection. Food consumption is reported as frequency of occurrence, aggregate percentage volume, and aggregate percentage dry weight. Dry weight (nearest 0.001 g) of foods was determined after drying at 60°C for 24 h.

After collection and removal of esophagus and proventriculus, birds were frozen for later analyses of body composition. Birds were thawed within six months of collection and weighed, measured, plucked, and dissected. We determined molt status of collected birds using methods similar to Heitmeyer (1987). Internal organs were weighed to the nearest 0.1 g on a top-loading digital scale. Contents of the gizzard, intestines, and ceca were removed and body and organ masses adjusted for these contents. The eviscerated carcass (lacking liver, heart, spleen, gizzard, kidneys, and intestines) was subsequently homogenized in a meat grinder (McLandress and Raveling 1981). A carcass sample of approximately 50 g was oven dried at 100°C for 48 h. Following drying, each sample was weighed to determine moisture content and then placed in a Soxhlet apparatus and lipids extracted for 48 h using petroleum ether as a solvent. The lipid-free sample was then weighed and ashed in a muffle furnace at 650°C for 24 h. Ash weight was subtracted from the lipid-free sample weight to obtain the ash-free lean dry mass (AFLDM), a measure of protein content (Raveling 1979).

Satterthwaite's approximation of the *t*-test (Snedecor and Cochran 1980:97) was used to compare sex ratio and pairing data between habitat types for each year. Time spent in each activity was compared without pooling data between years, sexes, and habitat types for each species using Mann-Whitney *U*-tests (Daniel 1978). Mann-Whitney *U*-tests were also used to examine differences between sexes for body and nutrient reserve masses.

RESULTS

Migration chronology, sex and pairing status, and habitat use.—Lesser Scaups migrated through the Klamath Basin from September through mid-November in fall 1985 and 1986 and from late January through April in spring 1986 and 1987 (Fig. 1). Bufflehead migration into the Klamath Basin was later in both fall (peak numbers occurred during late November and early December) and spring (peak numbers from mid–March through mid-April) (Fig. 1).

Eighty percent of Buffleheads were found on SF wetlands, while 61% of Lesser Scaups were observed on PF wetlands. Typically, a higher proportion of males was present in flocks on PF than on SF habitats for both species ($P < 0.05$) except for Buffleheads in 1987 ($P > 0.05$) (Table 1). Approximately 50% of female Buffleheads and Lesser Scaups were paired from late February to mid-March (Table 1). The percentage of paired females was not different ($P > 0.05$) between PF and SF habitat types.

Time budgets.—Buffleheads spent >60% of the day feeding (Fig. 2). Time spent in various activities by Buffleheads was not different ($P >$

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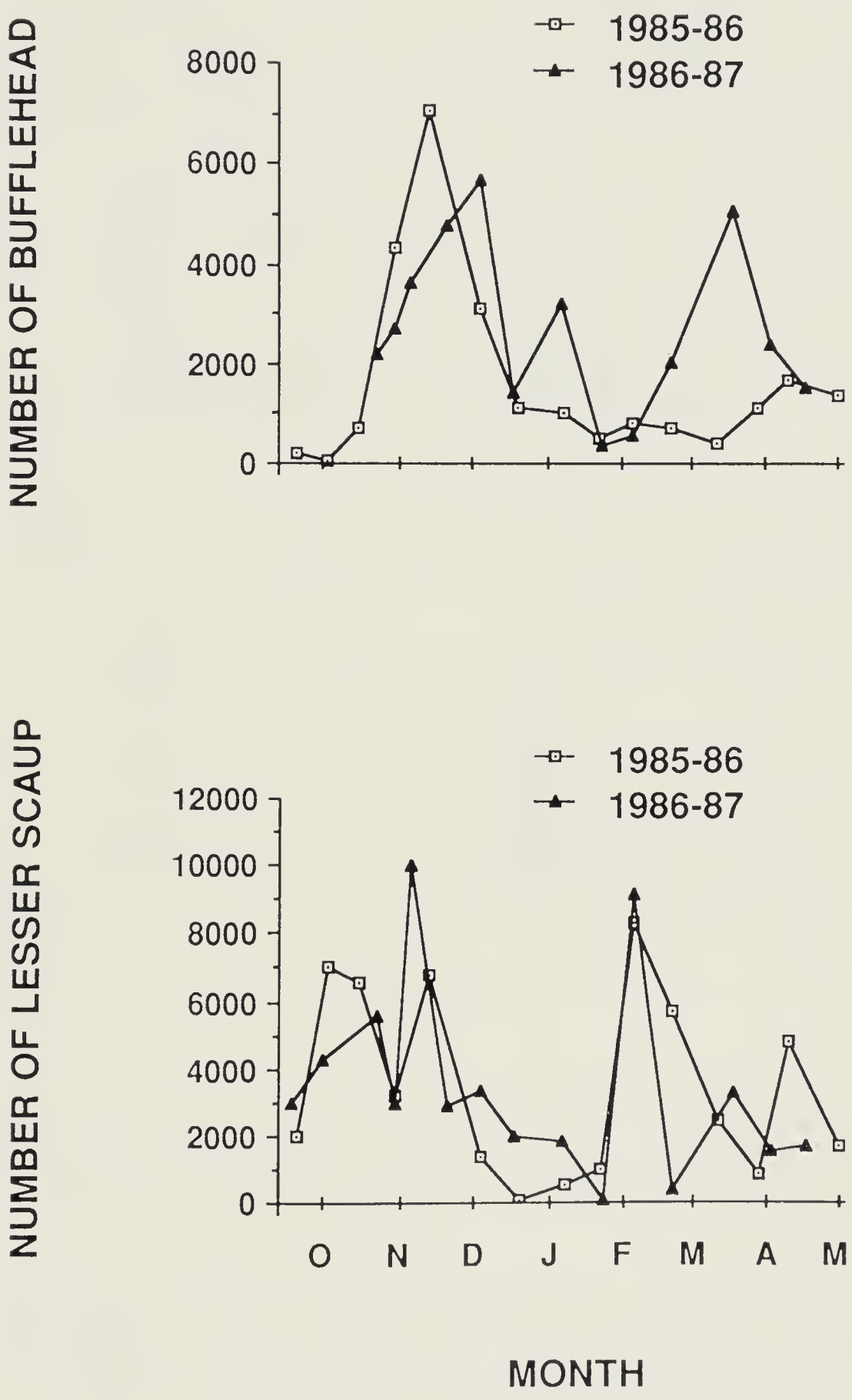
FIG. 1. Population estimates of Buffleheads and Lesser Scaups in the Klamath Basin, 1985–1986 and 1986–1987.


NUMBER OF BUFFLEHEAD
1985-86
1986-87
8000
6000
4000
2000
0
NUMBER OF LESSER SCAUP
1985-86
1986-87
12000
10000
8000
6000
4000
2000
0
O
N
D
J
F
M
A
M
MONTH

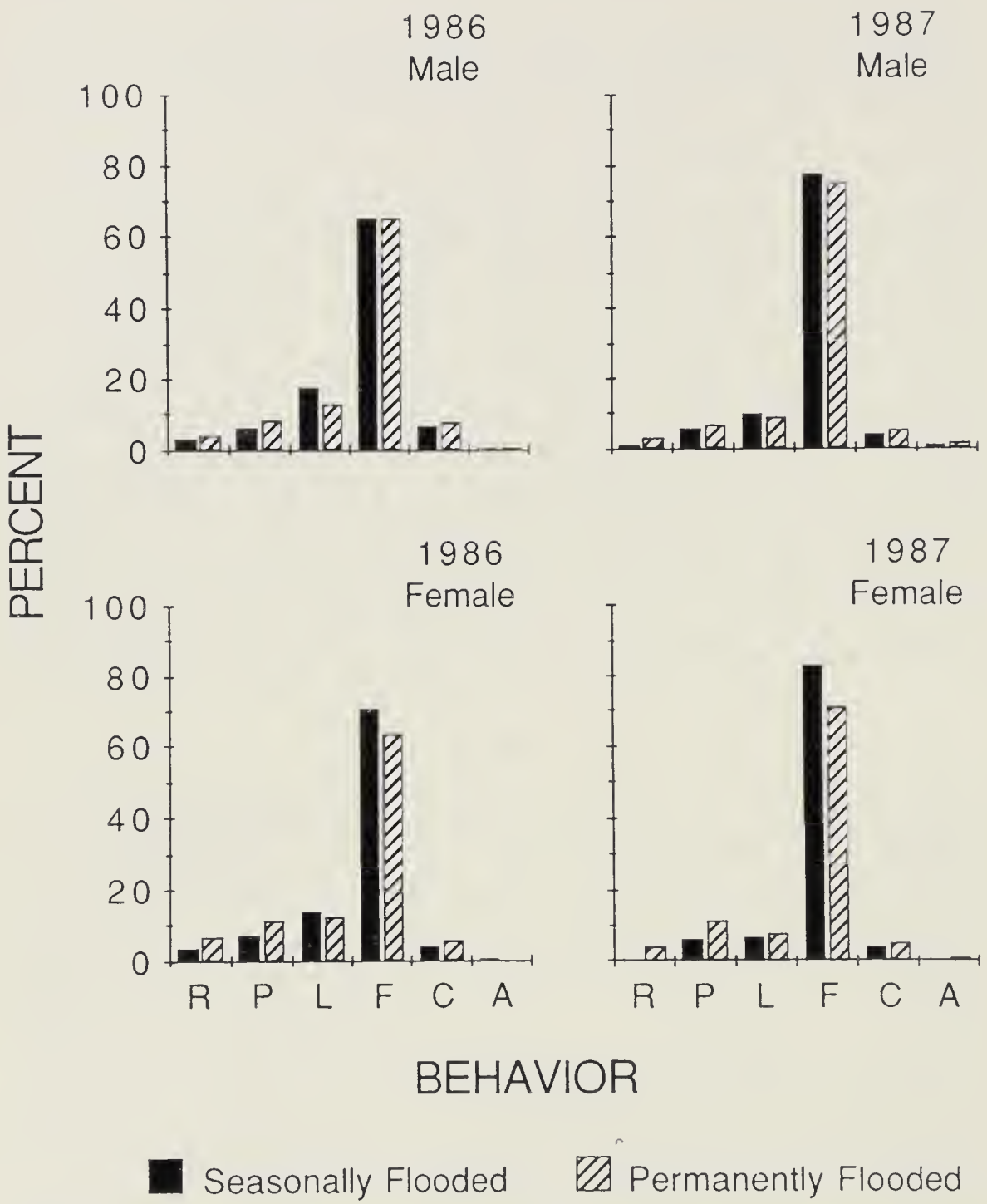


FIG. 2. Percentage of time spent by Buffleheads on seasonally and permanently flooded marshes at Lower Klamath National Wildlife Refuge in various activities during daylight hours. R = resting, P = preening, L = locomotor, F = feeding, C = courtship, and A = agonistic.

0.05) between years, sexes, or habitat types. Buffleheads were typically very active and spent little time (<10%) resting during daylight hours. Locomotor activity consisted mainly of birds swimming and flying to join feeding flocks or courtship parties. Three copulations were observed on

TABLE 1

PERCENTAGE OF MALES IN FLOCKS, AND PERCENTAGE OF FEMALES THAT WERE PAIRED, OF BUFFLEHEADS AND LESSER SCAUP OBSERVED ON LOWER KLAMATH NATIONAL WILDLIFE REFUGE IN SEASONALLY FLOODED (SF) AND PERMANENTLY FLOODED (PF) HABITATS IN SPRING 1986 AND 1987

Species and year	Percentage male			Percentage female paired		
	SF	PF	Combined	SF	PF	Combined
Bufflehead						
1986	58.1	63.9	59.0	53.5	56.1	53.8
	(34)[a]	(29)	(63)	(38)	(30)	(68)
1987	62.1	62.0	62.1	51.9	54.0	52.1
	(54)	(49)	(103)	(52)	(49)	(101)
Lesser Scaup						
1986	70.1	78.5	74.2	48.6	50.7	49.4
	(34)	(31)	(65)	(35)	(29)	(64)
1987	68.2	72.4	71.4	52.7	55.0	54.4
	(51)	(50)	(101)	(51)	(49)	(100)

[a] Number of flocks sampled in parentheses.

TABLE 2

ESOPHAGEAL AND PROVENTRICULAR CONTENTS OF BUFFLEHEADS COLLECTED ON LOWER KLAMATH NATIONAL WILDLIFE REFUGE IN SPRING 1986 AND 1987

Food item	Males (N = 4)			Females (N = 7)			Combined (N = 11)		
	O[a]	V	W	O	V	W	O	V	W
Animal	100	73	70	100	61	51	100	66	58
Chironomidae	100	13	12	86	28	18	91	22	16
Corixidae	25	40	29	43	21	14	36	29	20
Physidae	25	13	24	14	6	11	18	9	16
Planorbidae	25	2	2	14	1	4	18	2	3
Ostracoda	25	2	1	14	1	1	18	2	1
Gammaridae	25	2	1	14	1	tr	18	2	1
Dytiscidae				14	3	2	9	2	1
Plant (seeds)	75	27	30	86	39	49	82	34	42
Scirpus robustus	75	8	12	57	10	11	64	9	11
Polygonum lapathifolium	50	8	11	42	10	17	45	9	15
Scirpus acutus	50	4	4	14	3	2	27	3	3
Rumex spp.	75	4	1	14	1	tr	36	2	1
Potamogeton pectinatus	25	2	2	57	13	17	45	8	11
Chenopodium botrys	25	2	tr				9	1	tr
Carex spp.				14	1	tr	9	1	tr
Eleocharis spp.				14	1	tr	9	1	tr

[a] O = Percent occurrence, V = percent aggregate volume, W = percent aggregate dry weight, tr = trace.

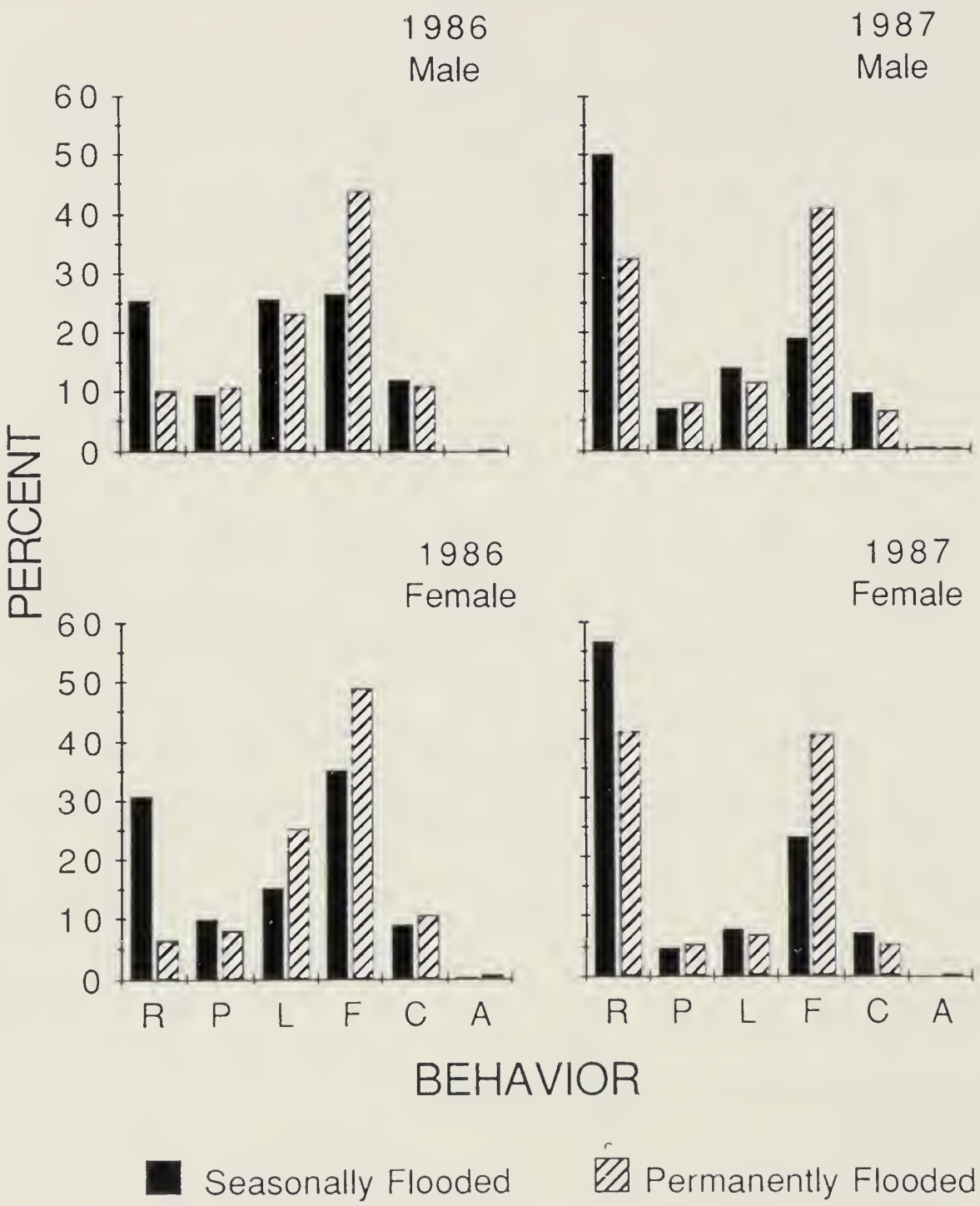


FIG. 3. Percentage of time spent by Lesser Scaups on seasonally and permanently flooded marshes at Lower Klamath National Wildlife Refuge in various activities during daylight hours. R = resting, P = preening, L = locomotor, F = feeding, C = courtship, and A = agonistic.

SF habitats. Common courtship activities included leading and following, head-bobbing, and pre- and post-copulatory displays. Aggressive interactions of males were mostly related to courtship.

Lesser Scaups spent more time resting and less time feeding during the

TABLE 3

ESOPHAGEAL AND PROVENTRICULAR CONTENTS OF LESSER SCAUPS COLLECTED ON LOWER KLAMATH NATIONAL WILDLIFE REFUGE IN SPRING 1986 AND 1987

Food item	Males (N = 6)			Females (N = 5)			Combined (N = 11)		
	O[a]	V	W	O	V	W	O	V	W
Animal	100	82	85	100	70	61	100	77	72
Chironomidae	83	50	63	100	34	33	91	44	46
Ostracoda	17	28	20	20	2	1	18	18	9
Planorbidae	33	3	2	100	14	12	64	7	8
Copepoda				20	12	5	9	5	3
Dytiscidae	17	1	1	20	4	2	18	2	1
Physidae				20	2	7	9	1	4
Daphnidae				20	2	1	9	1	1
Gammaridae	17	tr	tr				9	tr	tr
Plant (seeds)	83	18	15	80	30	39	82	23	28
Potamogeton pectinatus	33	7	6	40	16	27	36	10	17
Polygonum lapathifolium	67	5	4	40	4	2	54	5	3
Scirpus robustus	17	3	3	40	6	8	27	4	5
Rumex spp.	17	1	1	20	2	1	18	2	1
Scirpus acutus				40	2	3	18	1	1
Chenopodium botrys	17	1	1				9	1	tr

[a] O = Percent occurrence, V = percent aggregate volume, W = percent aggregate dry weight.

day than Buffleheads (Fig. 3). Time spent in all activities was not different ($P > 0.05$) between male and female Lesser Scaups. Lesser Scaups spent more ($P < 0.05$) time (>40% of the day) feeding in PF habitats than on SF habitats (<30% of the day) (Fig. 3). In contrast, scaups spent more time ($P < 0.05$) resting in SF habitats than in PF habitats. Lesser Scaups rested more in 1987 than during 1986 in both habitats ($P < 0.05$). Courtship among scaups usually consisted of ≥5 males courting one female. Agonistic behaviors by scaups were rare.

Food habits.—Buffleheads and Lesser Scaups consumed primarily (77% and 66% dry weight, respectively) animal matter while in the Klamath Basin (Tables 2, 3). Midge larvae (Chironomidae) were the most frequently consumed invertebrates and were present in 91% of both Buffleheads and scaups. Other foods commonly consumed by Buffleheads were water boatmen (Corixidae), physid snails (Physidae), and seeds of smartweed, alkali bulrush, and sago pondweed (Table 2). Lesser Scaups consumed many ostracods (Ostracoda), planorbid snails (Planorbidae), and sago pondweed seeds in addition to chironomids (Table 3).

Body condition.—All male Buffleheads and Lesser Scaups collected were paired, non-molting, and in Alternate plumage. All female Lesser Scaups

TABLE 4

CARCASS AND SELECTED ORGAN MASSES (MEANS ± SE IN G) OF BUFFLEHEADS AND LESSER SCAUPS COLLECTED ON LOWER KLAMATH NATIONAL WILDLIFE REFUGE IN SPRING 1986 AND 1987

	Bufflehead		Lesser Scaup	
	(N = 6) Male	(N = 7) Female	(N = 6) Male	(N = 5) Female
Fresh body	442 ± 37	333 ± 21*[a]	734 ± 24	663 ± 52*
Eviscerated carcass	311 ± 15	215 ± 21*	499 ± 34	438 ± 22*
Moisture	192 ± 19	136 ± 5*	298 ± 20	279 ± 17
Lipid	40 ± 15	26 ± 15*	78 ± 9	53 ± 27
Ash	10 ± 3	6 ± 2	17 ± 3	14 ± 1
AFLDM	70 ± 7	48 ± 5*	108 ± 5	92 ± 5
Right breast	37 ± 2	27 ± 2*	63 ± 3	58 ± 4
Right leg	16 ± 1	12 ± 1*	27 ± 5	24 ± 2
Liver	15 ± 3	12 ± 2	19 ± 1	19 ± 2
Gizzard	10 ± 3	8 ± 2	29 ± 1	26 ± 7
Intestine	12 ± 3	10 ± 1	31 ± 4	31 ± 4
Testes or ovary	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.1	0.2 ± 0.1
Oviduct		0.3 ± 0.1		0.2 ± 0.2

[a] Mann-Whitney *U*-tests (Daniel 1978) between sexes, * = $P < 0.05$.

were paired and in early stages of the prebasic molt. Five of the six female Buffleheads collected were paired and in early stages of the prebasic molt; the other female Bufflehead was paired, non-molting,and in Alternate plumage.

Absolute measures of body, eviscerated carcass, and moisture masses were larger for male than for female Buffleheads and Lesser Scaups; other organ and carcass composition masses were similar between sexes in both species except for lipid, AFLDM, right breast, and right leg masses in Buffleheads (Table 4). Buffleheads averaged 26–40 g lipid, while Lesser Scaups averaged 53–78 g lipid. Gonad and oviduct masses were small for both species.

DISCUSSION

Migration chronology of Buffleheads and Lesser Scaups through the Klamath Basin during our study was similar to that reported by Erskine (1972) and Bellrose (1980). Sex ratios observed in this study were also similar to those reported in other studies (Bellrose et al. 1961, Erskine 1972, Bellrose 1980). The percentage of paired females was generally higher, however, than reported for early spring in other studies and locations (Weller 1965, Erskine 1972). Our study occurred relatively early in spring migration for both species (Erskine 1972, Bellrose 1980) and all

but one of the birds we collected were adults; therefore, it appears that a large proportion of the first Buffleheads and Lesser Scaups migrating northward into the Klamath Basin in spring were paired adults. Earlier northward migration in spring by paired adults has been documented for some other waterfowl species, and may confer survival and reproductive potential advantages (McLandress and Raveling 1981, Heitmeyer 1988).

Wetland habitats in the Klamath Basin provide important food resources and resting areas for Buffleheads and Lesser Scaups. Spring migrant female Buffleheads and scaups incur overlapping nutritional costs of migration, courtship, and prebasic molt, and both species spent considerable portions of the day feeding. High consumption of invertebrates by Buffleheads and scaups in this study is consistent with other winter and spring food habits data for both species (Yocum and Keller 1961, Rogers and Korschgen 1966, Bartonek and Hickey 1969, Erskine 1972, Hoppe et al. 1986). Invertebrates, and chironomid larvae in particular, are heavily exploited by several waterfowl species (Gray 1980, Pederson and Pederson 1983, Woodin and Swanson 1989).

Relatively little is known about body and organ masses and nutrient storage patterns of diving ducks. Although sample sizes are small, data for this study suggest that Bufflehead and Lesser Scaup body masses in the Klamath Basin during spring are near winter levels (Ryan 1972, Joanen 1964, Erskine 1972) but below body masses upon arrival at northern breeding areas (Erskine 1972; Afton and Ankney unpubl.). However, comparative data for wintering or breeding scaup populations in the Pacific Flyway are needed for accurate interpretations of spring body mass data.

The above considerations emphasize the importance of spring migration sites, such as the Klamath Basin, to Buffleheads and Lesser Scaups. The continued loss of wetland habitats throughout North America (Tiner 1984) amplifies the need for enhanced management of high quality habitats on remaining areas. Further studies of diving ducks on spring migration areas are needed to elucidate evolutionary factors influencing chronology of annual events, patterns of nutrient storage, habitat use, and behavior.

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TERMINAL EGG NEGLECT IN THE AMERICAN WHITE PELICAN

ROGER M. EVANS[1]

ABSTRACT.—Brood reduction theory suggests that parents may allocate less care to their youngest, or terminal offspring because it has a lower potential reproductive value. The possibility that American White Pelicans (*Pelecanus erythrorhynchos*), which exhibit hatch asynchrony and a high probability of brood reduction, selectively neglect their terminal, or b-egg was examined by monitoring temperatures of artificial eggs. Before the onset of pipping, mean upper egg surface temperatures exceeded 37°C, and individual readings rarely fell below 36.0°C. After pipping of the a-egg, upper egg surface temperatures of the remaining (artificial) b-egg dropped significantly, and more individual readings fell below 36.0°C. A temperature gradient between egg top and bottom was present before pipping, but not subsequently. These results, along with evidence from a separate study indicating that hatching of pelican embryos is significantly retarded by moderate chilling, suggest that there is a potential for biologically relevant neglect of the terminal egg after pipping of the first egg in this species. *Received 24 Oct. 1989, accepted 1 Feb. 1990.*

There is growing evidence that incubation of the last egg to hatch in asynchronously hatching clutches of some ground nesting species may become disrupted as parents begin to tend to the needs of the first pipped or hatched members of the brood. Neglect of terminal eggs has been documented primarily in gulls and terns (Laridae) (Beer 1962, Drent 1970, Haycock and Threlfall 1975, Courtney 1979), and has been noted or suspected in some other species, including the American Coot (*Fulica americana,* Gullion 1954), South Polar Skua (*Catharacta maccormicki,* Spellerberg 1971), and Pied-billed Grebe (*Podilymbus podiceps,* Forbes and Ankney 1988). Although a quantitative theoretical treatment of terminal egg neglect is lacking, it is plausible that neglect is most prevalent in species that are known to exhibit brood reduction. Where loss of an offspring through the brood reduction process is likely, parents may be able to increase their own fitness by investing relatively less in the potential victim (Mock 1987), usually the last young hatched. Incubation neglect of the last-hatched egg by parents that are actively feeding or otherwise caring for older siblings can be viewed as a manifestation of differential parental care extending back into the late incubation period.

In the American White Pelican (*Pelecanus erythrorhynchos*), brood reduction affecting primarily the younger of the two siblings is virtually obligate (Cash and Evans 1986). Hatching asynchrony in this species

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averages about 2.5 days. When the first, or a-egg pips, its vocalizations cause the incubating parent to shuffle its webbed feet off the eggs (pelicans lack a brood patch and normally incubate eggs under the foot webs). Eggs are then pushed back between the legs for the remainder of the incubation period (Evans 1988a, 1989). At this time the eggs, no longer held in position by the parent's foot webs, are subject to exposure whenever the parent rises to preen or when it settles without covering a partially dislodged egg. Exposure is especially likely for the b-egg after the a-egg has hatched. Using temperature sensors implanted at the center of artificial eggs, I found (Evans 1989) that as a result of such exposure, the terminal b-egg was subjected to increasing variability and lower ranges in temperature as the hatch progressed, but mean core temperature was unaffected.

The above results provide conflicting evidence for terminal egg neglect in white pelicans: observations of increased egg exposure and the lower range of temperature of b-eggs after the a-egg pips suggest neglect, but the more stable mean core temperatures do not. To further examine the problem of terminal egg neglect in this species, I did preliminary tests (reported fully below) where I positioned a temperature probe on the upper surface of an artificial egg that was immovably fixed in position near the center of the nest. Before the onset of pipping of the companion a-egg, mean egg temperature recorded from this probe was higher than any of the mean temperatures previously reported for this species when probes were positioned at the egg center. After the companion a-egg pipped, upper surface temperatures fell back to a level similar to those previously obtained from the egg center, a result consistent with the terminal egg neglect hypothesis. These results also suggested the hypothesis that the temperature gradient, normally expected between top and bottom of a large egg (Drent 1970), may be less pronounced or even absent when incubation behavior changes upon pipping of the first egg. The objective of this study was to obtain additional egg temperature measurements to permit a closer examination of these hypotheses.

METHODS

Pelicans were studied at a colony of about 2600 nests (1989 census) at East Shoal Lake, Manitoba, Canada. Observations of courtship flights in April were used to predict the approximate date of hatching (Evans and Cash 1985), so that brief visits to the colony to install instrumented eggs could be delayed until the earliest nests were in the late stages of incubation, when the risk of desertion due to human disturbance is minimal. It was found that disturbance could be further decreased by making the final approach, of about 50 m, slowly on hands and knees.

All egg temperatures were taken from artificial eggs consisting of a natural pelican egg shell strengthened internally with a thin layer of fiberglass and filled with agar. These eggs have weight and thermal characteristics similar to fresh eggs (Evans 1989). In the preliminary

experiment, artificial eggs were fixed in position by inserting and gluing a wire, 10 cm in length, down from the bottom of the egg. When the protruding wire was pushed into the bottom of the nest, egg shifting or turning could not occur. For this data set, a thermistor bead probe, about 1 mm in diameter, was affixed with transparent tape to the upper surface of the egg approximately 2 cm towards the blunt end from the position of maximum diameter around the long axis of the egg. This probe location approximated the location of the pip hole in natural eggs. The lead from the probe was taken under the egg and thence under the nest rim and across the ground to a weatherproof instrument box located outside the limits of the colony, about 30 m from the nest being measured. Temperatures in this experiment were recorded every 5 or 10 min with a calibrated (±0.2°C) model SQ 2 4-channel data logger (Grant Instruments, Cambridge), with up to four different nests being monitored simultaneously. A total of 20 nests, 10 before pipping and 10 during and after hatching of the a-egg were measured. For the nests monitored during and after the a-egg hatched, it was found that the parents accepted the fixed eggs without problem provided they were put in position before the a-egg had actually hatched. Data reported here were for nests set up with late stage a-pip eggs that had always hatched before termination of data collection the next day.

In an attempt to make the eggs used for temperature measurements more natural, eggs used in the main experiment were not fixed in position. During their construction, a 16 g lead weight was glued to the inside of the shell to ensure a weight asymmetry. As described by Drent (1970) for natural eggs, weight asymmetry combined with parental billing of the egg during egg "turning" acts to ensure that the heavy side of the egg is usually downwards in the nest. These eggs were equipped with four temperature sensors, each consisting of a 30 ga Type T teflon-coated thermocouple wire with soldered tip covered by a bead of epoxy. Three independent sensors were implanted flush with the outer surface of the egg shell. As in the preliminary experiment each was approximately 2 cm towards the blunt end as measured from a circle around the point of maximum diameter on the longitudinal axis of the egg. These probes were positioned so that when the egg lay flat in the nest, heavy side down, one probe was up (0°), one down (180°), and one at the side (90°). A fourth probe was positioned at the center of the egg, to detect internally the presence of a gradient, if any, between top and bottom. The leads from each of the sensory beads proceeded into the egg, and thence out by a common hole drilled through the bottom, well away from the lower surface temperature sensor. Outside the egg, the four leads were taped into a single composite wire which exited through the nest bottom and out below the nest rim, leaving the egg essentially free to be moved about within the nest. Beyond the nest, thermocouple leads were tied to an embedded spike to ensure walking pelicans would not inadvertently pull the artificial eggs from the nest. Leads then continued on the surface of the ground to the instrument box as described above. Temperature measurements for the main experiment were recorded automatically every 5 min with a calibrated (±0.1°C) SQ 1203 8-channel data logger. The use of all 8 channels in this experiment made it possible to monitor simultaneously all probes from two eggs in different nests. Ten nests, two per day for five days, were monitored at each of three stages of incubation: (1) before pipping, when eggs were incubated under the foot webs, (2) after pipping of the a-egg, when the eggs were no longer held under the foot webs, and (3) after hatching of a-egg. No instances of rejection or failure to incubate the artificial eggs occurred at any stage.

Experimental protocol was similar for both experiments. At each nest, one egg was temporarily removed and replaced with the instrumented artificial egg. The usual routine was to enter the colony in the morning, turn off the data loggers, and verify that the probes and appropriate nest contents were in place. In the preliminary experiment, I then left the colony to download the data to a portable microcomputer, then repositioned the probes at new

nests upon returning about 2 h later. In the main experiment, probes were usually repositioned before leaving the colony to download, so that it was not necessary to enter the colony or cause any incubating pelicans to leave their nests when returning to reset the data loggers for the next run. Rare exceptions to this routine occurred when observations with binoculars or monitoring of current egg temperature indicated a problem with the nest contents that required correcting. In one instance, rain precluded normal nest checks, and the equipment was left in place for two days. Only the first day of data was used in analyses.

To reduce possible effects of my presence on egg temperatures and to ensure central egg temperatures had time to reach a steady state (Evans 1989), the first three hours of data and any readings logged after my arrival at the colony the next day were excluded from analysis. Readings were analysed for an average of 19.3 ± 0.6 h/nest in the preliminary experiment and for 16.0 ± 0.5 h/nest in the second. Descriptive statistics were computed for the readings for each probe from each nest. The means were then treated as single data points and subjected to higher order analyses following the computational methods of Bruning and Kintz (1968). Additional non-parametric tests, when needed for data sets that were non-normal, were done according to Daniel (1978).

RESULTS

Fixed eggs.—Before the onset of pipping, the overall mean upper surface temperature derived from the 10 individual means of the fixed artificial eggs was 37.4 ± 0.2 (SE) °C (average of 161 readings/nest), significantly warmer ($t = 5.87$, df = 18, $P < 0.001$) than the upper egg surface during and after the hatching of the a-egg (34.6 ± 0.4°C, 185 readings/nest).

To provide further insight into the possibility of egg neglect as the hatch progressed, the proportion of temperature readings equal to or greater than 36.0°C were also calculated for each nest. This particular temperature was chosen for analysis on the basis of incubator studies (Evans 1990) indicating that hatching of pelican eggs can be significantly retarded when pipped eggs are incubated at 33.0°C, but are not affected relative to controls when incubated at 36.0°C. The exact temperature between these two values where hatch retardation begins has not been determined. For present purposes, it was assumed that the relative proportions of readings above or below 36.0°C at a nest provides an estimate of the potential for biologically significant egg neglect. Before pipping, the median proportion of temperature readings per nest that was equal to or greater than 36.0°C was 89.9%, significantly greater (Mann-Whitney $U = 1$, $N_1 = N_2 = 10$, $P < 0.001$) than the median proportion of 22.0% achieved during and after the hatching of the a-egg.

Movable eggs.—Before the onset of pipping the overall average of the 10 nest means for the upper surface probes in movable artificial eggs was 37.2°C, essentially identical to the mean temperature obtained for the same incubation stage and probe location in the fixed eggs described above. Mean upper surface temperature of the artificial b-egg then dropped

TABLE 1
MEAN EGG TEMPERATURES FOR THREE PROBE LOCATIONS OVER THREE STAGES OF INCUBATION

Incubation stage[a] (mean readings/nest)	Probe location				
	Top surface	Egg center	Bottom surface	*F*	*P*
pre-pip (200)	37.2 ± 0.1	35.7 ± 0.2	34.8 ± 0.3	34.62	<0.001
a-pip (184)	35.6 ± 0.3	35.8 ± 0.3	35.9 ± 0.3	1.25	NS[b]
a-hatch (192)	35.0 ± 0.4	35.5 ± 0.2	35.3 ± 0.4	2.48	NS
F	13.75	2.62	0.37		
P	<0.001	NS	NS		

[a] Pre-pip = neither egg yet pipped; a-pip = a-egg pipped, b-egg not pipped; a-hatch = a-egg hatched, b-egg not yet pipped.
[b] NS = $P > 0.05$, N = 10 nests at each stage.

significantly when the a-egg pipped and hatched (Table 1). Egg center and bottom surface temperatures did not differ significantly.

Overall comparisons of egg temperatures among the top, bottom, and centrally located probes for all three incubation stages (pre-pip, a-egg pipped, a-egg hatched) were significant for probe position (two-way ANOVA, repeated measures on probe location, $F = 6.54$, df = 2,54, $P < 0.005$) and for interaction between probe position and incubation stage ($F = 19.33$, df = 4,54, $P < 0.001$). There was a definite temperature gradient through the egg from top to bottom during the pre-pip stage of incubation (Table 1). This temperature gradient was no longer present after the onset of pipping, when all probe locations took on mean readings between 35.0 and 35.9°C. The proportion of readings greater than or equal to 36.0°C followed a pattern similar to mean temperature (Table 2). Over 92% of readings equalled or exceeded 36.0°C on the upper egg surface during the pre-pip stage, while all other probes and stages were significantly lower.

Temperatures recorded by the probe located on the egg surface midway (90°) between the upper and lower probes did not differ significantly from those recorded from the egg center ($P > 0.05$). Mean temperatures for the 90° probe were: pre-pip = 35.8 ± 0.3, a-pip = 35.9 ± 0.3, a-hatch = 35.0 ± 0.4°C (compare to values for egg center, Table 1). During the pre-pip incubation period, the 90° surface probe did not track either the warmed upper surface or the cooler lower surface, but rather maintained an intermediate position within the gradient between top and bottom as did the center of the egg itself. Analysis of the magnitude of the pre-pip temperature gradient (temperature of upper minus lower probe) during successive 3-h periods between 1700 and 0800 h CDT indicated no sig-

TABLE 2

MEDIAN PROPORTION OF EGG TEMPERATURE READINGS ≥ 36.0°C FOR THREE PROBE LOCATIONS OVER THREE STAGES OF INCUBATION

Incubation stage[a]	Probe location			Chi-square[b]	*P*
	Top surface	Egg center	Bottom surface		
pre-pip	92.1	47.8	26.7	15.20	<0.001
a-pip	49.5	51.6	51.6	3.05	NS[c]
a-hatch	32.5	21.8	37.6	3.80	NS
H[d]	13.80	0.65	5.95		
P	<0.001	NS	NS		

[a] See footnote[a], Table 1.

[b] Comparison among probe locations for each incubation stage, Friedman's ANOVA by ranks, df = 2, N = 10 for each probe location.

[c] NS = $P > 0.05$.

[d] Comparison among incubation stages for each probe location, Kruskall-Wallis test, H distributed approximately as Chi-square, df = 2, N = 10 for each incubation stage.

nificant changes in relation to time of day (one-way ANOVA, repeat measures, $F = 0.7$, $P > 0.05$).

DISCUSSION

Results of both experiments show that the upper surface temperature of American White Pelican eggs is held at a relatively stable temperature of just over 37.0°C prior to the onset of pipping. Essentially identical results by the two different methods, employing fixed eggs and movable but weighted eggs, lends support to the conclusion that this temperature represents the actual biological temperature regimen applied to eggs by pelicans, at least during the latter portions of the pre-pipping incubation period when these measurements were taken. Because embryos were absent from the instrumented eggs, the upper surface temperature can be taken as that applied by the incubating parent independent of heat production and vocal feedback from the embryos. Mean incubation temperatures above 37°C are rare among birds (Webb 1987), and could indicate that pelican embryos are particularly sensitive to cooling.

Temperatures in the region of 35°C obtained for probes located at the egg center in this study are in close agreement with those reported for the same probe position in an earlier study of American White Pelicans (Evans 1989). The absence of a significant change in egg center temperature as pipping and hatching proceeded in both studies, despite the significant drop in upper surface temperatures at this time, appears to result from a combination of two effects: (1) the egg center temperature during the pre-

pip stage represents the approximate mid-point of the gradient through the egg from top to bottom, and (2) after pipping, the gradient is absent, as temperatures on all surfaces, upper, lower, and 90°, level out at or just above 35°C. That the latter temperature happens to be the same as the mid-range of the gradient during the pre-pip stage may be fortuitous, but in any event explains why a significant temperature drop at the upper egg surface can occur without being reflected at the egg center. As far as I am aware, the loss of the top-to-bottom temperature gradient with the onset of pipping has not been reported previously, but may be a general phenomenon in species where application of the brood patch to the eggs changes markedly at that time (e.g., Laridae, Beer 1962, Drent 1970).

During the early stages of incubation, avian embryos are small and tend to float to the top of the yolk, and so are positioned close to the upper egg surface (Drent 1970). Subsequently, the enlarging embryo takes up a transverse position adjacent to the air cell near the large end of the egg (Freeman and Vince 1974). Throughout this time, the upper egg surface temperature, and especially that lying towards the blunt end of the egg where the upper surface probe was positioned in these experiments, would correlate closely with the temperature actually attained by the embryo (Drent 1970). An incubation temperature of about 37°C may therefore be a close estimate of the temperature applied to the embryo throughout much, if not most, of the incubation period. Towards the end of the incubation period, when the embryo begins to fill more and more of the egg space, the upper portions of the egg towards the blunt end may still be the most relevant for the embryo, as the relatively inert yolk is concentrated at the lower side of the egg, especially near the small pole (Freeman and Vince 1974), where cooler temperatures would presumably have less of a retarding effect on development. It is relevant that artificial incubation of pelican eggs at the temperature usually used for domestic fowl, 37.8°C, results in a high percentage hatch of viable pelican eggs (Evans 1990).

The abrupt drop in upper surface egg temperature with the onset of pipping and hatching of the a-egg, and a corresponding decrease in the proportion of temperature readings in the "safe" region at or above 36.0°C supports the contention that the terminal, or b-egg in American White Pelicans is potentially subject to some degree of neglect after the a-egg pips. Evans (1990) found that a lowering of incubation temperature by an additional 3°C to 33.0°C during the pipped egg stage caused an increase of over 50% in the pip-to-hatch interval. This suggests that fairly minor amounts of egg cooling due to parental neglect could retard the hatching of b-eggs, causing them to lag farther behind the a-egg. Any increase in hatching asynchrony is potentially damaging to the younger sibling in

species exhibiting a high probability of brood reduction, as in the white pelican (Cash and Evans 1986). Additional manipulative field experiments are required to determine the amount of hatching delay and resultant fitness costs to the terminal egg arising from neglect under natural incubation conditions in this species.

The low b-egg incubation temperatures found in this study are in accord with the prediction that it would be adaptive for parents in brood-reducing species to invest relatively less in terminal offspring. Despite the inherent appeal of such an interpretation, it is important to emphasize that other, possibly non-adaptive interpretations may also account for terminal egg neglect in pelicans. It is possible, for example, that neglect of the b-egg during the final stages of incubation in this species arises because the parent, no longer holding the eggs under its foot webs, lacks adequate information about the true temperature state of the unpipped b-egg, and so is unable to regulate its temperature optimally. This interpretation is consistent with the suggestion (Evans 1988b, 1989; see also Drent 1970 and references), that once the b-egg pips, its vocalizations when cold could have the effect of reinstating normal incubation attentiveness from a cooperative parent. This possibility is under investigation.

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SHORT COMMUNICATIONS

Nesting of Golden Eagles in the central and southern Appalachians.—Many sources have asserted that Golden Eagles (*Aquila chrysaetos canadensis*) bred in the Appalachians as far south as North Carolina and Tennessee. There is little evidence to support these claims. Maine, New Hampshire, and New York are the only eastern states with confirmed Golden Eagle nesting records (Spofford 1971), and there is a mid-1800 record from Pennsylvania (see below). The species now breeds only in Maine, where nests have been reported as recently as 1986 (Andrle and Carroll 1988). In this note we review the published reports of Golden Eagles nesting in the central and southern Appalachians, and find no evidence of nesting in the area.

The notion that Golden Eagles nested in the southern Appalachians grew out of circumstantial associations. First, southeastern records indicated Golden Eagles have been sighted throughout the year. Secondly, adult and immature birds occasionally were seen together. Finally, Golden Eagles were seen at nest sites. Although fledglings were never sighted, and eggs never reported, the cumulative circumstantial evidence persuaded some authors to build a case for the nesting of Golden Eagles in the Southeast (e.g., Mengel 1965). Authors of non-regional publications independently drew from the regional sources of information to sketch the total nesting distribution of the Golden Eagle in North America and included the southern Appalachians in its range (e.g., Bent 1937; A.O.U. 1957, 1983; Palmer 1988). South of the Adirondacks, "evidence" of nesting is available only from one site in Pennsylvania and from one site in the Cumberland Plateau. All other accounts are from secondhand sources or are circumstantial (see below), and, except for one 1902 record, the five reports with specified dates are from between 1934 and the early 1940s. The lack of verifiable evidence does not eliminate the possibility of individual pairs of Golden Eagles nesting sporadically throughout the central and southern Appalachians; however, it certainly makes all records suspect.

Below we have summarized the literature concerning the nesting status of Golden Eagles in the southeast. One remarkable feature of the summary is that since the first mention of "Golden Eagles" possibly nesting in the southeast by Audubon in 1831 (in Kentucky at the mouth of the Green River), no ornithologist has personally reported seeing nesting Golden Eagles. The lack of first hand accounts, especially considering the extent of coverage of the southern Appalachians by pioneer bird students (Brewster 1886, Cairns 1889, Burleigh 1941, and many others) and the high profile and nest-site loyalty of Golden Eagles, weaken the idea that Golden Eagles nested in southeastern United States. Furthermore, despite the large number of naturalists and commercial collectors who collected bird eggs from mid-1800s to the 1940s and the relatively large assemblage of egg sets from this period that made their way into museum collections, there is not a single set of Golden Eagle eggs from south of the Adirondacks. Surely, if nesting sites were known, Golden Eagle eggs would have been collected. For example, the historic distribution of Peregrine Falcons (*Falco peregrinus*) in the same area can be partly reconstructed from data associated with the collection of egg sets (e.g., McNair 1988).

Many statements concerning the nesting of Golden Eagles in the southern Appalachians are based on the local presence of birds "throughout the year" or during the nesting season. Because these eagles take four years or more to reach maturity, the presence of birds during any season does not constitute nesting. Furthermore, adults from elsewhere in North America, whose nesting attempts have failed, are likely to wander, and there is some evidence that they appear at certain sites during spring lambing season (see below). Also, birds regarded

as adults may be subadult individuals because of the similarities in plumage. Field guides and similar aids showing plumage progression were not available during the period when most of the presumed nesting activity was taking place. Bird students in the southern Appalachians would have had little experience with either of the North American eagles, and some reports probably refer to immature Bald Eagles (*Haliaeetus leucocephalus*). (Note, for example, Audubon's 1831 report for Kentucky.)

Other statements concern eagles associated with cliff nests. There are no specific references to birds sitting on nests, feeding young in nests, or carrying nesting material. Almost no nest-associated records are from the known nesting season (April through July to mid-August for Maine, Spofford pers. obs.). In fact, there are no descriptions of any nest, so the nests involved could have been those of Bald Eagles, Peregrine Falcons, Red-tailed Hawks (*Buteo jamaicensis*), Common Ravens (*Corvus corax*), or perhaps other, cliff-nesting species.

The only "evidence" for nesting in the southern Appalachians is the mention of "four young birds" captured and "two birds" collected from a nest (Brooks 1944, Bent 1937, see below). The capture of four young Golden Eagles in West Virginia would be an incredible number of young from a single nest, and the capture of four young from different nests in the same county in the same year is equally unlikely. Bent's (1937) record of two birds collected from a nest is doubtful. Data with the specimens does not clearly match Bent's (1937) statements (see below). Nevertheless, these reports represent the only rationale for a 800 mile (1290 km) southern extension to breeding distribution of Golden Eagles in the eastern United States.

Another problem with the possibility of Golden Eagles nesting in the southeast is that for the most part, natural foraging habitat for these eagles is absent from the southeastern United States in general and from the central and southern Appalachians in particular. Stupka (pers. comm. to George Hall) doubted the existence of breeding Golden Eagles in the Great Smoky Mountains because of the unavailability of open habitats. The clearing of land for agriculture could have allowed Golden Eagles to expand briefly their nesting range. They may have nested in the Southeast in isolated sites that offered protected nesting ledges and artificially maintained foraging habitat. Open, wind-swept mountain balds of the southern Appalachians do attract Golden Eagles, apparently because they offer open areas in which to hunt. With few exceptions, however, these areas are small, widely scattered, limited in number, and not successionally stable, and it is unlikely that they could sustain nesting pairs and their growing young.

The following is a state-by-state summary of the literature concerning the presumed breeding of Golden Eagles in the central and southern Appalachians.

Pennsylvania.—There are no nesting records cited by recent authorities. Van Fleet (1884) stated that the Golden Eagle "quite certainly breeds in Clearfield County." Beck (1924) reported on a nest of Golden Eagles along the Susquehanna River prior to the 1850s in "A Chapter on the Ornithology of Lancaster County, Pennsylvania." The eyrie was on a cliffside opposite the mouth of the Peqvea River and thus appears to have been in York County. The observation was reported by Dr. M. W. Raub, a known ornithologist of the period. Beck regarded the species as a "former rare resident." The Susquehanna River eyrie has apparently been overlooked by recent authors.

West Virginia.—Hall (1983) states "There is no definite evidence that the species ever nested in the state, but four young birds were captured by a hunter near Dunmore, Pocohontas County, in 1934 (Brooks 1944), and there are many summer reports. . . . It seems likely that even now, in the 1980s, this species does on occasion nest on some remote mountain cliff."

Maryland.—No nesting records are available. Stewart and Robbins (1958) consider the species a transient.

Kentucky.—Mengel (1965) considered Golden Eagles to have probably nested in Kentucky in early times, but he had no evidence for the state. He cited an account by Audubon (1831) under Bald Eagle. Audubon (1831) described a pair of "Birds of Washington" on a cliff near the mouth of the Green River and concluded that they were not young "White-headed Eagles" because of the cliff site (Bald Eagles are now known to occupy such sites). As noted by Mengel, Audubon's description of the birds catching and eating fish rules out the possibility that they were Golden Eagles.

Virginia.—Murray (1952) states "The author has good reason to think that a pair nested about 1935 at the Devil's Backbone, near Crabbottom, Highlands County. [C.O.] Handley, Jr. was told by local people that until the early 1940's a pair had nested on the western face of Massanutten Mountain in Shenandoah County." In 1975 it was reported that Golden Eagles had "no firm breeding records but possibly has nested in Giles, Highlands, Shenandoah, and Washington cos." (Larner 1975). Palmer (1988) states that "most recent active nest in SE U.S. presumably in Giles Co., Va in 1952." This record was from Spofford's files but was misinterpreted and is not valid. Despite much talk of a supposed nesting on Little Stony Creek in Giles Co., there is no substance to the reports and the supposed observer later confirmed to Spofford that no nest was found.

North Carolina.—There is no nesting evidence, although the birds are believed to have nested in the state. Pearson et al. (1959) noted "There have long been rumors that these eagles breed in our higher mountains, but we know of no eggs or eaglets having been recorded." Powell (1968) listed about a dozen places named after eagles (not including several referring to family names of early settlers). Most are in the mountains in the western portion of the state along major water courses. Eagle Creek (Swain County) was named "from the fact that a nest of eagles was found near its head" (near Fontana Lake). Several other sites are named Eaglenest (Eaglenest Branch, Eaglenest Creek, Eaglenest Mountain, and Eaglenest Ridge [the latter three sites are associated with, and named after, each other]). Thus, while there is no doubt that eagles formerly nested in the southern Appalachians, the proximity to major water courses suggests that all may refer to Bald Eagle nest sites.

Tennessee.—There are no conclusive records of nesting and there are only a few records for the state. Dubke (1964) noted that individuals appeared on Roan Mountain around lambing time and stayed for about a month. The birds appeared again in the fall. Alsop (1972) regarded Golden Eagles as "presumed breeders" but had no evidence of nesting. Ganier (1973) reported that Golden Eagles visited Tennessee during the winter and that a few bred in the escarpments of the Cumberland Plateau and on cliffs in the high mountains along Tennessee's eastern border. He stated that he had been unable to find any occupied nests in either of these areas in the last 50 years "but found several old nests." There is a single unsexed Ganier specimen from Moore County, near Lynchburg (LSU 75702) collected on 12 April 1935, and the label reads "one of a pair." Bent (1937) noted "I have two birds in my collection that were taken from a nest on Walden's Ridge, in the Cumberland Mountains, Tenn., in 1902. . . ." However, Raymond Paynter informs us that the two specimens from Bent's collection (MCZ 252,795; 252,796) were collected in July and thus would represent very late breeding season specimens. Since young Golden Eagles may not leave nest sites until they are 10 weeks old, July does not rule out nesting, but if this species nested this far south, it seems reasonable that the nesting phenology should be in advance of birds in Maine, which leave nest in July. The Bent specimens were said to have been "raised in captivity for over a year," indicating they were young birds, but according to Paynter both are adults. The year of collection suggested by Bent (1937) is 1902, and the date on the tags is also 1902, so there was likely some confusion as to at least the date of capture.

After his account of Golden Eagle records in the Great Smoky Mountains, Stupka (1963) concluded "Normally, neither the Golden nor the Bald Eagle breeds in the type of envi-

ronment which prevails in the park, even though some of the early writers published comments to the contrary. The guide who directed Charles Lanman [1849] to Alum Cave Bluff in 1848 stated that the first time he came to this place he decided to climb a steep face at the north end of the formation, 'opposite to an eagle(s) nest, where the creatures were screaming at a fearful rate.' In spite of the considerable difference between the size of an eagle and of a Peregrine Falcon, the writer is of the opinion that the latter, and not the former, bird was encountered there. Lemoyne (1886) purloined the journal of a friend in which there is an account of the killing of a pair of Golden Eagles at their eyrie in Blount County and the collecting of two eggs. This report is referred to by Rhoads (1895) and Ganier (1926), but the latter, in his correspondence with me (1973), had serious doubts regarding Lemoyne's narrative. Cairns (1902) and Brimley (1940) state that these birds breed on the cliffs of the higher mountains in western North Carolina, but they give no particulars and it is assumed that the information is second-hand." Additionally, regarding the Alum Cave Bluff record, we would like to note that unlike Peregrine Falcons, Golden Eagles do not "scream" at intruders. They glide silently away to a remote perch.

South Carolina.—No nesting records are available, although Wayne (1910) and Sprunt and Chamberland (1949) both suggested that Golden Eagles may nest in the mountains of northwestern South Carolina. They knew of no authentic nesting record for the state.

Georgia.—No nesting records. Burleigh (1958) noted, "I was told of a nest found on the slopes of Brasstown Bald some years ago that was said to have been an eagle nest, but, unfortunately, there was no possibility of verifying that statement."

Alabama.—No nesting records (Imhof 1976).

Although it is not possible to disprove the occasional past nesting of Golden Eagles in the southeast, it is also apparent that the bird's breeding has not been documented and that the information that is available is unconvincing. On the other hand, the current literature has not addressed the unsubstantiated nature of the records, so it is possible that persons with photographs of active nests or other irrefutable information are simply unaware of its importance and, therefore, have not shared it with the ornithological community.

Furthermore, we would like to point out that even in the northeastern United States, the historic nesting of Golden Eagles was never adequately documented nor completely understood. For example in Eaton's (1911–1914) "Birds of New York State" there is a comment that Dr. William Ralph is the authority for the statement that the eggs have been taken in New York. However, there is no record of this, and such a rare and spectacular find would have been widely known. While Ralph's statement is apparently true, even in heavily worked New York state, the only published record, until 1957, was Audubon's 1833 account of a site in the Hudson River highlands of a pair that bred for nine successive years in the same crevice of rocks. Yet between 1955 and 1960 field investigations turned up five or six active nest sites in the Adirondacks. In the long overlooked pre-1850 nest record from the Susquehanna (Beck 1924), Witmer Stone, who proofread the manuscript, commented that this was probably the last stand of the Golden Eagle in eastern North America. Stone was apparently unaware of a nest with two young found in 1876 on White Horse Ledge at Conway, New Hampshire (Allen 1903). Thus, even in areas where Golden Eagles are now known to have nested, the confirmation of historic information was slow in coming, and at least several unquestionable published reports had been overlooked.

Unless more evidence becomes available, we suggest that authors use discretion in discussing the nesting status of Golden Eagles in the east south of New York. Because current authors are still suggesting that Golden Eagles nested in the southern Appalachians, well-intentioned persons have been trying to "reintroduce" the species into the southeast and to manage open habitats for their foraging. Hopefully, the information provided here will foster reconsideration the "re"-establishment efforts made on behalf of the Golden Eagle in the southeast.

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Notes on Gray Jay demographics in Colorado.—The social organization and population dynamics of the Gray Jay (*Perisoreus canadensis*) are not well known. Most literature on the Gray Jay is anecdotal, consisting primarily of casual field observations or more detailed observations of one or very few individuals over a period of days or weeks (e.g., Warren 1899; Skinner 1921; Lawrence 1947, 1968; Rutter 1969; Burnell and Tomback 1985). To describe accurately the social and population structure, more long-term studies are required. The value of long-term studies of larger populations of jays has been clearly demonstrated by Woolfenden (1975), Woolfenden and Fitzpatrick (1984) and Brown (1963a, b, 1987). The objective of this paper is to provide an initial report of an ongoing demographic and behavioral study of Gray Jays in the northern Colorado Rocky Mountains. We provide information on survivorship based on mark-resight data, movements, and group size and composition. This report is based on field data obtained over eleven years of sporadic data collection; however, it provides the best information presently available on long-term patterns of Gray Jay social organization.

Materials and methods.—This study was conducted in the Colorado State Forest (CSF), which is 152 km west of Fort Collins on the west slope of the Medicine Bow Mountains, at an altitude of 2500–3800 m. The habitat is open pine forest on west and south-facing dry slopes below 2900 m and closed pine-spruce-fir forest interspersed with grass meadows on north slopes and above 2900 m. Three primary banding sites were established, approximately 3.2 km apart, within a 23-km^2 study area. Site #1 was located at North Michigan Reservoir; Sites #2 and #3 were north and east of the reservoir. Sites #1 and #2, located at

small CSF campgrounds, were established in 1979; Site #3 was more isolated and was established in 1986. All three sites were located at 2700–2800 m elevation. Based on our banding efforts and observations, each site was used concurrently by two to four distinct groups of Gray Jays. Gray Jays were trapped using two-cell Potter traps and a variety of baits. Occasionally, tapes of various Gray Jay vocalizations were used to attract jays to the immediate area of the traps. Each individual was marked with a permanent, numbered U.S. Fish and Wildlife Service aluminum band and a unique combination of plastic, colored, leg bands. These colored bands allowed individual identification of birds at operational distances using binoculars or a spotting scope. Individual Gray Jays were recognized from their colored leg bands during periodic surveys from 1979 to 1989. Positive identification was made whenever possible by re-trapping birds and reading the USFWS aluminum band numbers. These surveys, until recently, were made primarily in the summer and fall months when the study site was readily accessible. Since fall 1986, increased access and personnel have allowed a more intensive effort to band and locate jays during winter and spring months when approximately 1–2-m-deep snow blankets the area.

Gray Jay nesting occurs in late February and March (Brewer 1879, Bradbury 1918, Hurlbutt 1932, Bailey and Niedrach 1932); therefore, minimum longevity calculations were made by assuming that jays banded in adult plumage during summer months were hatched in March of the previous year, while birds in juvenile plumage were assumed to have been born in March of the current year. Jays on our study area cannot be reliably aged after October of their birth year due to their fall molt into adult plumage. Mark-resight survivorship estimates were calculated using the Kaplan-Meier product-limit estimation technique (Kaplan and Meier 1958) and were based on the minimum number of quarters (three month periods, beginning in January) a bird was known to have survived on the study site. Those individuals located in the past year were considered alive (unless death was confirmed) and were classified as "closed" in the Kaplan-Meier calculations. It was assumed that all birds that disappeared had died. Population size was estimated using Jolly-Seber estimators (Nichols et al. 1981), in which relocations were equated with recaptures of individually banded jays. Group size and composition were summarized by number, age class, and season (quarter).

Results and discussion.—Average longevity of a Gray Jay after banding as an adult (N = 86) was 2.8 years (median = 1.7 years). For those banded as juveniles (N = 27), the average longevity after banding was 1.6 years (median = 0.7 years). The maximum longevity, including minimum back-calculation to birth date, is seven years, nine months. The longevity record for Gray Jays is ten years, two months (Clapp et al. 1983); however, we feel that this was based on an incorrect assumption, that Gray Jays retain their juvenile plumage for at least 1.5 years. In the original report, Farner (1947) made no such statement and claims a minimum age of nine years. In our experience with western Gray Jays, juveniles reach full adult measurements in five months (July) and are indistinguishable from adults in color after 1 October. If our assumption of adult plumage after October is correct, then the minimum age of the Farner bird is nine years, five months.

Minimum age survivorship curves for the jays banded as adults (unknown age) and juveniles (known age) are shown in Fig. 1. Survivorship is higher for birds banded as adults, a finding expected but not found in Scrub Jays (Woolfenden and Fitzpatrick 1984). Survivorship of adult and juvenile Gray Jays in Colorado appears to be much lower than Scrub Jay breeders in Florida (Woolfenden and Fitzpatrick 1984). This may be due to higher mortality in Gray Jays or may simply reflect a more transient species or population. We believe, based on the literature and movement and dispersal information described below, that higher mortality due to the relatively harsher sub-alpine environment of the Rockies is the more likely possibility.

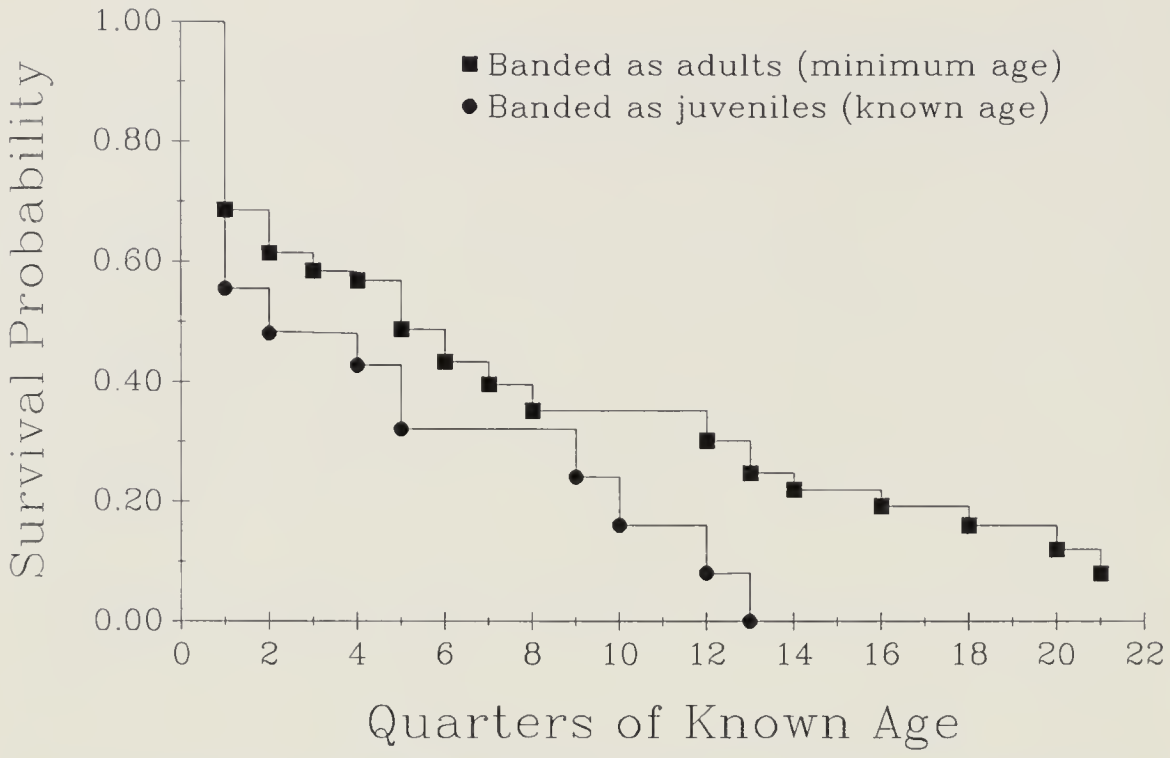

FIG. 1. Kaplan-Meier survivorship curves for Gray Jays in northern Colorado. Birds banded as adults are of unknown age (minimum-age survivorship) while birds banded as juveniles are of known age (known-age survivorship).

Low nesting success and high early mortality of juveniles is indicated by the fact that only 42% of mated pairs had one or more juveniles with them in the July–September quarter (pairs with one juvenile = 27%; two juveniles = 15%). By the October–December quarter, only 19% of pairs still had juveniles (pairs with one juvenile = 17%; two juveniles = 2%). No dispersal of juveniles at these times of year was recorded.

Dispersal movements of Gray Jays appear to be very limited. After 169 person-days of censusing of 116 jays banded in this study area, no band recoveries were made at an appreciable distance from the site at which the jay was banded. Mean maximum distance from banding site for adult jays was 264.6 m (range: 86–858 m; N = 34) and for jays banded as juveniles was 208 m (range: 18–522 m; N = 13). There is no significant difference in these distances ($P > 0.05$, two-way ANOVA). Mean maximum distance was significantly lower at the more isolated Site #3 (mean: 169.99 m vs 298.15 m at two other sites; $P = 0.014$, two-way ANOVA), probably because this site was more heavily forested than the other sites. We hypothesize that there was more usable forest habitat near the capture site at Site #3 and less need to move long distances. This also meant that jays were more difficult to locate and identify at a distance. In summary, birds in this population were relatively stationary, with territorial vacancies into which juveniles can move occurring frequently due to relatively high mortality (Fig. 1).

Overall population size, based on Jolly-Seber estimators for the pooled data from all three banding sites, averaged 27.6 birds from 1982 through 1988 (range: 18.0–50.9). While this initially appears to be a large variation in population size, 80% of this variation between years was explained by a regression against person-days in the field for a given years ($r = 0.89$; $P \leq 0.05$). Mean group sizes for each season and age class (Table 1) are independent of census effort. Group sizes stabilized at approximately 2.3 for the winter months (Jan.–

TABLE 1
AVERAGE GROUP SIZE OF GRAY JAYS, TABULATED BY AGE CLASS AND SEASON

		Jan.–Mar.	Apr.–Jun.	Jul.–Sep.	Oct.–Dec.
Adults	Mean	2.3[a]	2.2	2.3 (2.3)[b]	2.1 (1.7)
	SD	0.9	0.9	0.9 (0.8)	1.1 (0.7)
	N	16	12	48 (20)	40 (8)
	Range	1–4	1–4	1–4 (1–4)	1–7 (1–3)
Juveniles	Mean	—[c]	—	0.6 (1.3)	0.2 (1.0)
	SD			0.7 (0.5)	0.5 (0.0)
	N			48 (20)	40 (8)
	Range			0–2 (1–2)	0–2 (1–1)
Total	Mean	—	—	2.9 (3.7)	2.3 (2.9)
	SD			1.1 (0.9)	1.1 (0.8)
	N			48 (20)	40 (8)
	Range			1–5 (2–5)	1–7 (2–4)
Percentage of single bird groups		0.19	0.08	0.12	0.17

[a] Group size values include repeated sightings of the same groups across, but not within, quarters and years.
[b] In parentheses are values for groups which contained young of the year.
[c] It is impossible to distinguish juveniles from adults during the January through June period.

Mar.). This was generally a mated pair with occasionally a surviving juvenile or an unrelated adult jay ("third bird" of Rutter 1969). Single birds constituted 8–19% (no seasonal difference) of the groups while groups of four or five (a mated pair, one or two juveniles of the year, and another adult jay) occurred in 12% of groups. The unrelated, adult "third birds" were loosely associated with, and subordinate to, all other members of the group. As expected, the number of juveniles in groups which successfully fledged offspring decreased from the third to the fourth quarter of the year (Fig. 1), but interestingly, the number of adults in the group decreased as well (Table 1).

Our preliminary data concur with those of Rutter (1969) that Gray Jays exhibit a monogamous and territorial mating system. Less than one-fifth of mated pairs raise one or two juveniles to independence, and the juveniles remain on the natal territory through winter. Movements of jays are limited, and survivorship on the home range is very low. An interesting aspect of the social organization is the presence of "third birds," adults apparently unrelated to the mated pair which reside on the territory for most of the year. The role of these "third birds" is unclear, but neither Lawrence (1947) nor Rutter (1969) reported nest helpers in Ontario Gray Jays. Intense monitoring of one nesting in our study area indicated no nest helping by a third bird present on the home range of the nesting pair throughout the nesting period (Henry pers. comm.).

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Nest-site selection by Boat-tailed Grackles.—Female birds that choose nest sites that maximize their reproductive success should have a selective advantage. If females choose nest sites predictably, males may be able to monopolize females in the same sense that predictable resources can be monopolized by an individual (e.g., Brown 1964). It is therefore

important to examine environmental and biotic influences on female distribution in order to understand fully the mating system in a population (Wolf and Waltz 1988). In this paper I examine the factors influencing nest site choice by female Boat-tailed Grackles (*Quiscalus major*). In Florida, Boat-tailed Grackles commonly nest in cattail marches, although their nests are also found in buttonbush, willow, and palm trees (Bancroft 1987, Dunham 1988). Male Boat-tailed Grackles are territorial, but where females build nests extremely densely, males are apparently unable to defend exclusive territories (Bancroft 1987). I first show that nest site choice occurs and then examine the effects of that selection on nest success. Predation on nest contents is a major cause of failure among marsh-nesting birds (Kale 1965, Post 1981, Orians 1980). In this study, predation is implicated as the most important factor determining nest site choice.

Methods.—I studied five marshes in northern Hillsborough County, Florida between 1 March and 20 June 1987. These were: Adventure Island retention pond (AI), Bearss Extension pond (BE), Burrell Lake (BL), East Burrell Lake (EB), and Lake Forest (LF). The primary emergent vegetation on all marshes was cattail (*Typha* spp.), with willow (*Salix* spp.) and buttonbush (*Cephalanthus occidentalis*) along the shores in some places. AI and EB were retention ponds dug by humans; BL, BE, and LF were marshes modified by man.

Every week until 12 May, marshes were searched from a canoe for new nests. Usually I visited nests every three days to record nest contents; the longest interval between visits was seven days. Nests that had been torn down were assumed to have been depredated by large mammals such as raccoons (*Procyon lotor*). Nests were torn down on all marshes, suggesting that these predators were not deterred by the presence of alligators. If scat or chewed remains of eggs or nestlings were found in the nest, I considered rats responsible. Both rice rats (*Oryzomys palustris*) and black rats (*Rattus rattus*) were present in the marshes. No damage and no remains in the nest suggested predation by Fish Crows (*Corvus ossifragus*) or rat snakes (*Elaphe obsoleta*).

Nest-site characteristics that may affect predation include nest visibility, distance from shore, distance from open water, height of the nest above water, and depth of water under the nest (Willson 1966, Lenington 1980, Burger 1985). To estimate nest visibility to both avian and terrestrial predators, I counted the number of stems at nest height within 0.5 m of the nest. Cattail stems were separated into new and old; new cattails were completely green, whereas old cattails had turned, or started to turn, brown. I used two estimates of visibility from above: height of vegetation above the nest and amount of light reaching the nest (Westmoreland and Best 1985). The vertical distance from the bottom of the nest to the average height of the surrounding vegetation was measured to the nearest 10 cm. The light incident on each nest was measured with an incident light photometer between 11:00 and 13:00 EST, while the sun was nearly straight overhead. I checked light level in the open frequently, and light intensity at the nest is expressed as a percentage of direct sunlight.

The distance of each nest from the shore and from the nearest area of open water greater than 1 m across was measured to the nearest meter. Water level in each pond was recorded at each visit. Water depth at the nest and height of the nest bottom above water were calculated by adding or subtracting the change in water level between the day the nest was built and the day measurements were taken at the nest. Southwest Florida Water Management provided data on water levels from past years, from which average monthly water fluctuation was calculated.

Nests supported by more plant stems should be less likely to be blown over by the wind. The number and type of stems supporting the nest were counted.

I compared nest-site characteristics to characteristics of the available habitat in order to demonstrate nest site choice (Johnson 1980). Available habitat was determined as follows. Fifty 1-m^2 plots on each marsh were chosen randomly. In each plot, the number of old and

new cattail stalks with at least 30 cm exposed above the water in a 1-m diameter circle were counted. Depth of water, height of cattails above water and light intensity at breast height were measured in the center of each plot. Distance to the shore and nearest open water from the center of each plot were determined from a map (see below).

I compared nest-site characteristics to the characteristics of the entire marsh using the Kolmogorov-Smirnov test (D. H. Johnson pers. comm.). This method shows which habitat is preferred relative to the habitat available; it does not indicate absolute habitat preference.

At the end of the study, marshes and nests were mapped using an alidade, stadia rod, and plane table. Distances between nests, from nests to shore, and from random plots to shore were measured from these maps.

Results.—I found 371 nests on the five marshes studied. Of these, 21 never contained eggs. An approximately equal number of nests were in cattails adjoining the shore and on cattail islands (islands: 176 nests, shoreline: 156 nests). Almost half (45.7%) of all nests fledged young, and 75.8% of nest failure was caused by predation. I found scat from black rats in 15 nests, eggshell fragments in 51 nests, and chewed nestling remains in 12 nests (12 nests contained both scat and eggshell or nestling remains). In total, rats ate the contents of 48.6% of the depredated nests. The second most common cause of failure was flooding (17.7% of failed nests). A 7-day period of rain between 28 March and 4 April raised water levels as much as 53 cm (BE). The resulting variance in water level was greater than the 29-year variance for March or April on local lakes (March: $F = 1.65$, April: $F = 2.02$; $P < 0.05$). Because 54.2% of the nests active on BE at that time were flooded, the marsh was deleted from further analyses. Only 4.9% of all nests were abandoned (9.1% of failed nests). Of the 371 nests, two failed because they were built in cattails that tipped, and two were constructed in such a way that eggs or young fell out.

Nests were in denser cattail and deeper shade than random sites on all four marshes (Kolmogorov-Smirnov, $P < 0.01$) and farther from shore than random sites on three marshes (LF, BL $P < 0.05$; EB, $P < 0.01$). Cattails were shorter around nests than on random sites (EB and LF, $P < 0.05$), and nests were farther from open water than were random sites (AI, $P < 0.01$, BL, $P < 0.05$).

Nest sites used did not differ between marshes (ANOVA, all $P > 0.05$). Therefore, I combined data from all marshes to test for differences between successful and unsuccessful nests. Successful nests differed significantly from unsuccessful nests in six of the 12 characteristics measured (Table 1). Most of these characteristics also differed between nests depredated by rats and successful nests (Table 1).

Discussion.—Rice rats are major predators on bird nests in Georgia and Florida marshes (Kale 1965, Post 1981). In this study as well, half the nests that failed were depredated by rats, both rice rats and black rats. Rice rats are good swimmers and climbers (Wolfe 1982), and black rats climb well but are reluctant swimmers (van den Brink 1967). Rice rats nest in salt marshes (Post 1981), but I found no rat nests in the freshwater marshes I studied. Rats probably nested on shore and traveled out into the marsh each night; thus rat predation was more common on nests close to shore than on nests far from shore. Higher nests were safer, suggesting that rats were swimming out to nests or climbing near water level. Predation was higher on nests built in older cattails than on nests built in newer cattails, suggesting that rats spend more time in old cattail stands. Cattails that have aged and turned brown are sturdier than young green cattails and may be easier for rats to climb. Another possibility is that rats use regular paths through the cattails and are reluctant to explore new areas.

Rat predation was more likely on nests over deeper water than average. This may simply result from the fact that rat predation was most common on the two deeper marshes in the study. Older cattail stands are taller than young cattail stands ($P < 0.001$, Kolmogorov-Smirnov test).

TABLE 1

NEST-SITE CHARACTERISTICS FOR SUCCESSFUL AND UNSUCCESSFUL NESTS OF BOAT-TAILED GRACKLES IN THE TAMPA BAY REGION OF FLORIDA, ALL FOUR MARSHES COMBINED[a]

Characteristic	Median successful	Median unsuccessful	Predator		
			Snake	Rat	Raccoon
Total stem density[b]	141	146	139	140	149
New cattail density[b]	82	72[d]	40	61[d]	76
Old cattail density[b]	49	69[d]	69[c]	73[d]	71
Woody stem density[b]	0	0	0	0	0
New cattail support (number)	10	9	10	8	7
Old cattail support (number)	7	8	8	8	9
Woody stem support (number)	0	0	0	0	0
Water depth (cm)	91	99[d]	95	106[d]	105
Nest height (cm)	51	44[d]	51	42[c]	34[d]
Cattail height (cm)	140	145	140	160[c]	130
Distance to open water (cm)	140	100[c]	100	100	70[c]
Distance to shore (m)	5.7	5.2[c]	81	56[d]	84
Light intensity (% of direct sun)	37.5	33.0	24	35	68[c]

[a] Nests that never contained eggs excluded.
[b] Number per 1 m diameter circle.
[c] Different from successful nests at $P < 0.05$, Kolmogorov-Smirnov test.
[d] Different from successful nests at $P < 0.01$, Kolmogorov-Smirnov test.

Nests may be visible from water level if they are near open water, especially if the surrounding cattails are less dense. Successful nests were farther from the open than were nests that had been torn down. All but one nest that had been torn down was closer to the water than the average successful nest.

Depredated nests that contained no remains were in denser old cattail than successful nests. Sturdy old cattails may be easier for a snake to climb or more likely to hold the weight of a Fish Crow landing on the nest.

Water levels in the area commonly fluctuate 6–8 cm in March and April, posing little threat to nests (see also Bancroft 1986). However, the unusual week-long storm during peak breeding showed the potential importance of flooding. Unfortunately, nest height could not be compared to any characteristic of random sites. Nests built high enough off the water to avoid the flood clearly were more likely to be successful than were nests that got wet. However, even when flooded nests were removed from the analysis, lower nests were less likely to fledge young.

Females chose nest sites with characteristics that males might be able to predict. This predictability could allow territorial behavior to be economically feasible, as long as nests are not too tightly clumped. Nest site choice had a positive effect on reproductive success; that is, nests were more likely to be successful at preferred sites. Rat predation was the form of nest failure most strongly affected by nest-site characteristics, which suggests that nest sites may be selected to minimize the impact of rat predation.

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Turkey Vulture food habits in southern Ontario.—Where Turkey Vultures (*Cathartes aura*) live sympatrically with other New World vultures (Cathartidae), they forage individually or in widely scattered small groups and usually feed on small carcasses (Rabenold 1983, Paterson 1984, Houston 1986, Coleman and Fraser 1987). However, where Turkey Vultures

breed in the absence of other vultures, no data are available on their foraging ecology. My principal objective, therefore, is to provide new information on Turkey Vulture foraging ecology in this part of their range. My secondary objective arises from the opportunity provided by studying Turkey Vultures in allopatry with respect to other vultures. Diet assessment of vultures often relies on analyzing regurgitated pellets collected at roosts. Since Turkey Vultures often roost with Black Vultures (*Coragyps atratus*), previous studies have been unable to distinguish between pellets produced by the two species (Yahner et al. 1986, Coleman and Fraser 1987). Because all pellets in my study area are from Turkey Vultures, I can determine whether the shapes and sizes of Turkey Vulture pellets are species-specific and evaluate Turkey Vulture diets more precisely.

Study area and methods.—Fieldwork was conducted near Milton in the Halton Region of southern Ontario. Approximately two-thirds of the land remains as farmland and wooded areas; the rest is urban. Two roosting sites were located in forests owned and operated by the Halton Region Conservation Authority. The first was situated at the bottom of Nassagaweya Canyon within Rattlesnake Conservation Area. At this site, vultures roosted in seven large sugar maples (*Acer saccharum*) and one large beech (*Fagus grandifolia*). The second roost was located approximately 5 km north of the first roost, at the edge of a 35-ha water reservoir within Hilton Falls Conservation Area. At this site, vultures used several large trembling aspens (*Populus tremuloides*) growing at the base of a 9-m cliff. Observations of foraging groups were made opportunistically from a car from 10 June through 7 October 1984 and from 9 April through 12 October 1985, between 11:00 and 16:00 h EST. Following Rabenold (1983), birds were considered to be in the same foraging group whenever they were observed in the air within 1 km of one another. Foraging observations were made at a distance of at least 1.6 km from the nearest known roost in order to avoid confusion with roost arrivals and departures.

Vulture pellets (N = 200) were collected from the two roosting sites between 11 June and 4 October 1985. A sample of 63 pellets (33 from Nassagaweya Canyon and 30 from Hilton Falls) were selected at random to determine dietary composition and relative frequency of food types used by vultures in this region. Pellets were air-dried, measured using calipers to nearest mm, weighed with an electronic balance to the nearest mg, and soaked overnight in water for dissection. A random sample of 100 hairs was removed from each pellet and cuticular impressions were made (Williamson 1951). A regional reference collection and hair guide (Adorjan and Kolenosky 1969) were used to identify mammal hairs microscopically. All mammal species were identified by hairs alone, while non-mammal species were identified by diagnostic parts (e.g., feathers) found in pellets.

Results.—Turkey Vultures in Ontario foraged solitarily in 56% of my observations (Table 1). This pattern differed significantly from the results of observations made in North Carolina (Stewart 1978, Rabenold 1983), where Turkey Vultures forage in larger groups (Kolmogorov-Smirnov, two-sample test; both P's < 0.001).

Because carrion varies in digestability, data from pellet analyses may not indicate the importance of particular food items. Nonetheless, they do allow comparisons of carrion used by Turkey Vultures among regions. Turkey Vultures in Ontario consume a variety of carrion types (Table 2). Only domestic fowl and woodchuck occurred in more than 50% (N = 31) of the pellets. Ninety-four percent of the pellets I analyzed contained two or more species, compared to 26% found by Paterson (1984) ($\chi^2 = 55.33$, $P < 0.001$). Overall, this represents a greater variety than reported for other areas.

To test for differences in the size of carcasses fed on by Turkey Vultures in Ontario and those living in other regions, all identified prey species were grouped, according to average live weight, into the size classes used by Coleman and Fraser (1987). Small species (<10 kg) were found to have a frequency of occurrence of 82%, medium species (10–20 kg), a

TABLE 1
COMPARISON OF TURKEY VULTURE FORAGING GROUP SIZE BETWEEN SOUTHERN ONTARIO AND NORTH CAROLINA

Group size	Number of times observed					
	Southern Ontario (this study)		North Carolina (Stewart 1978)		North Carolina (Rabenold 1983)	
	N	%	N	%	N	%
1	79	56.4	18	27.6	100	29.5
2	35	25.0	21	32.3	116	34.2
3	8	5.7	16	25.0	46	14.1
4	9	6.4	8	12.3	30	9.0
5	—	—	2	3.1	17	5.0
6	3	2.1	—	—	9	3.1
7	2	1.4	—	—	6	2.1
8	—	—	—	—	5	1.5
9	—	—	—	—	1	0.3
10	—	—	—	—	3	1.0
11	1	0.7	—	—	1	0.3
12	2	1.4	—	—	—	—
13	—	—	—	—	4	1.2
20	1	0.7	—	—	—	—
21	—	—	—	—	1	0.3
Mean group size =	2.11		2.31		2.75	

frequency of 13%, and large species (>20 kg), a frequency of 5%. Comparisons with studies in Virginia (Paterson 1984) and Pennsylvania and Maryland (Coleman and Fraser 1987) revealed that Turkey Vultures in Ontario fed significantly more on small carrion ($\chi^2 = 22.58$ and 32.84, respectively; both P's < 0.001). Sixty-two percent of the animal groups detected were of wild origin. Both Paterson (1984) and Coleman and Fraser (1987) found a significantly greater reliance upon domestic carrion in sympatric populations ($\chi^2 = 3.88$, $P < 0.005$; and $\chi^2 = 5.60$, $P < 0.025$, respectively).

Discussion.—Turkey Vultures in Ontario forage in smaller groups, feed on the carrion of smaller species, and feed proportionately more on wild species than has been found elsewhere. In addition, the number of species identified per Turkey Vulture pellet in Ontario exceeds that found in pellets collected in the mid-eastern United States.

Lower population densities of Turkey Vultures in Ontario, relative to more southern parts of their range, may be responsible for the small size of foraging groups I observed, whereas differences in diet between regions may be attributable to several factors. First, because the pellets of Turkey and Black vultures are not distinguishable, Paterson's (1984) sample may have included pellets from Black Vultures. Both species use the roost from which Paterson (1984) collected pellets (Fraser, pers. comm.). Thus, the analysis of Turkey Vulture diets may have been confounded in this study. Second, Coleman and Fraser (1987) collected their data by radio-tracking vultures to feeding sites which, as they note, may preclude the observation and identification of very small carrion that is consumed. Radio-tracking may also be biased towards the detection of completely digestible food items such as livestock afterbirth and offal, food sources which would not be detectable by pellet analysis. A third

TABLE 2

PERCENT OF TURKEY VULTURE PELLETS FROM SOUTHERN ONTARIO IN WHICH FOOD TYPE WAS FOUND (N = 63)

	%
Non-mammal	
Feathers (primarily *Gallus gallus*)	68
Invertebrates (primarily Coleoptera)	24
Vegetation	100
Mammal—domestic	
Dog (*Canis familiaris*)	2
Horse (*Equus caballus*)	2
Pig (*Sus scrofa*)	10
Cow (*Bos taurus*)	8
Bison (*Bison bison*)	3
Sheep (*Ovis aries*)	3
Mammal—wild	
Opossum (*Didelphis marsupialis*)	2
Shrew (Soricidae)[a]	27
Mole (Talpidae)[a]	8
Raccoon (*Procyon lotor*)	18
Striped Skunk (*Mephitis mephitis*)	18
Red Fox (*Vulpes fulva*)	2
Woodchuck (*Marmota monax*)	53
Red Squirrel (*Tamiasciurus hudsonicus*)	3
Grey Squirrel (*Sciurus carolinensis*)	2
Beaver (*Castor canadensis*)	2
Meadow Vole (*Microtus pennsylvanicus*)	2
Muskrat (*Ondatra zibethica*)	13
Eastern Cottontail (*Sylvilagus floridanus*)	9

[a] Possibly more than one species in the family present.

alternative for the differences in diets found in different studies is that the diets may reflect the carrion size-classes most readily available in each location. A detailed inventory of carrion availability in each study area would be necessary to assess the merit of this explanation.

Perhaps more interesting than the differences between Turkey Vulture diets in Ontario and elsewhere are the similarities. Overall, Ontario Turkey Vultures retained the small foraging group size and reliance on small carrion typical of this species where it is sympatric with Black Vultures. Both Stewart (1978) and Coleman (1985) have suggested that competition between the two species forced Turkey Vultures to exploit the small group-small carcass niche.

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Marking passerine tail feathers with colored tape.—Numerous techniques have been used to mark small birds, thus enabling them to be recognized at a distance when resighted (for a review see Marion and Shamis 1977). These methods have included colored leg bands, colored streamers, patagial tags, and coloring or marking plumage. Among the latter group are various schemes to mark the tail feathers (rectrices) of birds.

Colored leg bands have been used widely to mark birds, particularly for studies in open habitats with relatively short and/or sparse vegetation. Leg bands work best for species that can be approached closely and that do not conceal their legs when perched (Samuel 1970, pers. obs.). In "closed" habitats with dense tree and shrub cover, and for species often only sighted in flight or whose legs are not easily seen when the bird is perched, other, more visible markers (streamers, patagial tags, marking plumage, etc.) have been developed. Generally, more handling time and greater skill are required when these markers are applied to birds than when colored leg bands are used. Also, there may be a greater risk of a bird being injured either during the marking process or after its release (e.g., Hewitt and Austin-Smith 1966, pers. obs.).

In the past, tail-marking techniques have included painting or dyeing the rectrices (e.g., Swank 1952, Samuel 1970), imping feathers to the tail (e.g., Heydweiller 1934, Wright 1939), notching the rectrices (e.g., Lovell 1948), and applying tape to the tail (e.g., Dickson et al. 1982). In general, tail-marking techniques are less appropriate for species with relatively short tails or for species that use their tails in behavioral displays. Dyeing the tail of species with dark rectrices is not effective unless the feathers are first bleached. Such a procedure is cumbersome and generally not used. Painting the rectrices may require prolonged handling time to dry the paint before the bird is released, and the marker visibility is relatively short-lived because birds can preen the paint from the tail (Dickson et al. 1982, pers. obs.). Imping feathers to the tail is time consuming for passerine-sized birds (Hester 1963) and has been used mostly for game birds and raptors.

An alternative procedure for marking birds' tails involves using colored, plastic tape. This was attempted on Northern Cardinals (*Cardinalis cardinalis*) by Dickson et al. (1982). They cut the barbs from the rachis on the distal portion of a single rectrix and applied colored tape face-to-face on both sides of the rectrix. The tape was then trimmed to the same shape as the other rectrices. The technique was considered unsuccessful, however, because the birds bit off the taped portion of the rectrix.

In this report, I describe a procedure, not previously reported, for marking the rectrices of passerine-sized birds with tape. This marking technique is relatively quick and easy, requires inexpensive and readily available materials, is adaptable to birds of different sizes, and produces a highly visible marker that may persist until the tail feathers are molted. Furthermore, the marker is concealed from above when the bird is perched or sitting on a nest, and the taped rectrices do not seem to interfere with normal behavior. The method is particularly suited for marking birds to be studied during the breeding season. Details of this procedure and a discussion of its relative merits are the subject of this report.

Description of marking procedure.—This procedure consists of marking the rectrices with Scotch brand 471 vinyl plastic tape manufactured by 3M (see also Frankhauser 1964). The tape is sold in rolls ¾ inch (1.9 cm) wide and 36 yards (33 m) long, and is available in 10 colors (white, yellow, orange, red-orange, red, purple, blue, green, brown, and black). The tape is commonly found in stores that sell office supplies. The only other equipment required is a small pair of scissors and some means of holding the captured birds. The method has been used successfully to mark Northern Cardinals, Brown Thrashers (*Toxostoma rufum*), and Northern Mockingbirds (*Mimus polyglottos*).

Birds to be marked were mist netted and transferred to nylon holding socks during the marking operation. Each holding sock was made so that it fit over the bird's head and body, but allowed the legs and tail to protrude. The two or three outermost rectrices on each side of the tail were selected for marking, and the following procedure was used to mark first one side of the tail and then the other. (The procedure for two rectrices will be used as an example.)

The two outermost feathers on one side of the tail are separated from the other rectrices and positioned such that their rachises are lying side-by-side, with the outermost rectrix most ventral (Fig. 1A). This is the normal spatial relationship of the two feathers when the tail is folded. Placing the rachises side-by-side rather than superimposing one on the other adds lateral stability to the tape marker. A rectangular notch is then cut from the feather vanes on each side of the rachises about midway along the feather shaft (Fig. 1B). The length of the notches should be twice the width of the plastic tape (1.5 inches [3.8 cm]), and the notch on each side should extend from the edge of the feather vane to within 1–3 mm of the nearest rachis. The distance of the cut from the rachis depends upon the width of the vane; enough of the vane must be cut to assure adequate tape-to-tape contact (see below). This is particularly true for the outer, narrow vane of the rectrices.

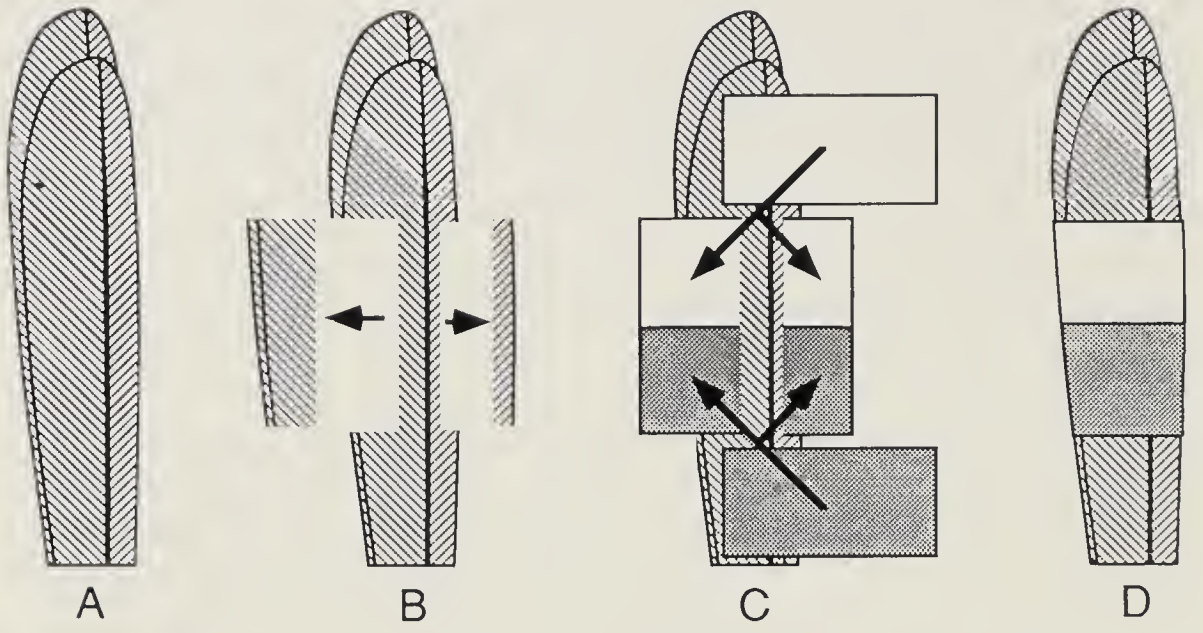

FIG. 1. Procedure used to mark birds' tails with colored, plastic tape. (A) Position feathers to be marked, (B) Notch vanes on both sides of rachises, (C) Attach tape strips to rachises in notched area, and (D) trim tape to feather contour. The ventral view of the right side of the tail is illustrated.

With the notches cut out, two strips of tape are attached (one anterior to the other) to the dorsal surface of the two rectrices and within the notched area (Fig. 1C). The strips of tape are applied one at a time, and they can be of different colors to provide a bicolor identification code. The tape should be cut in strips long enough to extend beyond the margins of the feather vanes. Two additional strips of tape are placed on the ventral side of the rectrices, directly over the two strips previously attached. Colors of the ventral strips of tape should match those of the dorsal strips. The strips of tape are then pressed firmly together to provide secure attachment to the rachises and assure good tape-to-tape contact in the notched areas of the vanes. Care must be taken at all times when handling a bird, and particularly when applying the tape, not to pull on the rectrices in a direction away from the bird's body, because that may cause the feathers to be shed during the marking operation or shortly after the bird is released.

The final step consists of trimming the strips of tape to conform to the contour of the edges of the two rectrices being marked (Fig. 1D). When marking is finished, the feather vanes and the tape should lie in the same plane, and the marked feathers should rest in a natural position when the tail is folded. Also, the bird should be able to fan its tail without restriction.

Evaluation of marking procedure.—The outermost rectrices were selected for marking because they are positioned beneath the innermost rectrices when the bird's tail is closed. This conceals the markers from above when the bird is perched or sitting on a nest—a highly vulnerable position to visually searching predators. The tail markers are visible from the side when the bird is perched, particularly when it flicks its tail. Although in the bird's shadow, the markers also can be seen from below when the tail is closed. Thus taping tails might be particularly useful in identifying birds, such as warblers, that spend most of their time in the upper canopy of trees. In general, the bands on the tail are much more easily seen and their colors more readily identified than those of the relatively small, colored leg

bands. When the birds are in flight, they sometimes fan their tail, making the colored tail markings highly visible. This is especially true when a bird is about to land. It is possible to recognize individual birds observed only in flight, and often only a fleeting glimpse is necessary to sight the colored markers, particularly the brighter colors.

Although the plastic tape is available in 10 colors, some colors work better than others. Light, bright colors (e.g., white, yellow, orange, red) are more easily identified than darker colors (e.g., black, green). This is particularly true when the birds are sighted only briefly (e.g., when vegetation is dense) or when light conditions are poor.

The number of rectrices selected to be taped on each side of the tail depends upon several considerations. At least two feathers are needed to provide lateral stability to the tape so that it does not rotate around the feather rachises, thus maintaining a flat and continuous surface between the feather vane and the tape. Taping more than one feather also increases the structural support for the tape and reduces the likelihood that the feather will pull loose during handling or after the bird is released. Also, there is a risk that the bird will remove the tape marker if only one rectrix is used (see Dickson et al. 1982). Taping more than three rectrices on each side of the tail probably would not add appreciably to the tape's stability, but it might increase retention of the marked feathers (see below). Taping more than three rectrices would, however, make the tape more visible from above when the bird is perched and would restrict the bird's ability to fan its tail during flight or other behaviors.

Tail taping is most appropriate for species with relatively long tails. For such species, two strips of colored tape can be seen easily from a distance, and possibly even a third strip of colored tape could be added and used effectively. Using colored tape to mark rectrices may not be a useful technique for birds with short tails, such as meadowlarks (*Sturnella* spp.) and European Starlings (*Sturnus vulgaris*), but the method has not been evaluated for such species. One advantage that marking the tail has over use of colored streamers is that the spatial order of the colors is maintained (i.e., one color is anterior to the other) thus doubling the number of bicolored identification codes that can be produced from a fixed set of colors.

Marking rectrices with tape does not seem to adversely affect birds' behavior. Passerines normally have 12 rectrices (Welty and Baptista 1988:23), thus the marking procedure reduces 12 separate feather "units" to 10 or eight depending upon whether two or three rectrices are taped on each side of the tail. Marked birds can fly normally and fan their tails, and the taped feathers fold in nicely with the other rectrices when the tail is closed. Marking rectrices may not be appropriate for birds that use their tail in courtship displays (e.g., Rufous-sided Towhees [*Pipilo erythrophthalmus*]; Dickinson 1968), but this needs to be evaluated.

The tape persists on the marked feathers because the birds evidently cannot pull it free from the rachises. This is probably attributable to the care taken to assure tape-to-tape contact on the outer edges of the tape strips. Northern Cardinals, with their strong beaks, are notorious for removing markers (e.g., Lovell 1948, Dickson et al. 1982, pers. obs.), but this was recorded in only one of seven cardinals marked with tail tape. In this instance, a male cardinal, recaptured 30 days after he was marked, was found to have removed all but one strip of tape from his tail. (The same bird also had removed one of two colored leg bands.) Most passerine-size birds have weaker beaks than cardinals, thus tape removal by these birds would be less likely.

Feather retention is the most important factor influencing duration of the taped-tail markers. (This probably is true for other tail-marking techniques as well.) Care must be taken not to pull on the rectrices during the marking operation, thus lessening the likelihood that the feathers will be dropped. Mitigating this loss, however, is the fact that the two sides of the tail are marked separately, thus rectrices must be lost from both sides of the tail before the marker is completely gone. It is possible that the birds themselves may remove some of the marked rectrices after their release when they attempt to pull the tape from the

tail. This would be most likely with species that have strong beaks, such as Northern Cardinals. To date, the taped-tail markers have been attempted on a relatively small sample of birds (14 Brown Thrashers, seven Northern Cardinals, and one Northern Mockingbird), thus further study evaluating the retention of marked feathers in these and other species would be desirable.

Marking rectrices with tape is a relatively easy technique to master, and for a cardinal-sized bird, it takes less than 5 min to complete. The technique would be appropriate for studies conducted during the breeding season or for other short-term studies where marker loss during molt would not interfere with research objectives. That the marker is lost at the end of the study period could be an advantage. This would reduce the likelihood of injury to the bird or of increased vulnerability to predators after the study period—hazards that may occur with other more permanent markers (e.g., streamers, patagial tags).

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Within-forest preferences of Wood Thrushes wintering in the rainforest of southern Veracruz.—Given current concern over the effects of tropical deforestation on wintering, nearctic, migrant species, we should ascertain how migrants distribute themselves within forests. Several tropical resident species have been shown to prefer treefall gaps in tropical forests (Willis and Oniki 1972, Stiles 1975, Gradwohl and Greenberg 1980, Schemske and Brokaw 1981, Levey 1988). Investigations of the within-forest distribution of wintering migrants which utilize tropical forest understory are scarce and rather inconclusive (e.g., Wunderle et al. 1987, Levey 1988). Here we present evidence for within-forest habitat (microhabitat) preference in the Wood Thrush (*Hylocichla mustelina*) on its wintering grounds in southern Veracruz, México.

Study area and methods.—The study was conducted during the boreal winters of 1983–1984, and 1984–1985 in the Sierra de Los Tuxtlas of southern Veracruz, México. Our main study site (8.75 ha, elev. 150 m) was located near the village of La Peninsula de Moreno (hence La Peninsula), in the Coxcoapan River valley, approximately 5.5 km ENE of the town of Coyame (Lago Catemaco). A second site (1.75 ha) on the slopes of the Volcán Santa Martha (approx. 15 km ESE of the La Peninsula site, elev. 470 m) was studied only during 9–19 March 1985. Both sites were located within primary rainforest (see Winker et al. 1990). Standard nylon mist nets (12 × 2.6 m) were placed 50 m apart on a 25-m grid system, and opened when weather permitted (both sites). Sampling various microhabitat types was not a focus of our main investigation (Rappole et al. 1989, Winker et al. 1990), and the areas sampled by individual nets occurred solely as a result of the location of a grid point. The 48 nets on the La Peninsula site were set in an 8 net by 6 net grid pattern, and were oriented perpendicular to the Coxcoapan River valley (approximately 50°). These nets were opened by block (either 12 or 16 nets) on a rotation basis to ensure relatively even sampling. Sampling periods included Oct. 1983–Jan. 1984, Nov. 1984–Mar. 1985. Nets were categorized subjectively as sampling "gap," "intact forest" or "mixed forest." Gaps are evident in forest through an increase in light levels, near-ground level vegetation (approx. 0–3 m), or, usually, both. Gaps on our site were present due to treefall, stream passage, or steep slopes. "Intact forest" was forest with a closed canopy and rather open understory. The "mixed" category was used when a net could not be confidently placed in either of the extreme categories due to the proximity of both microhabitat types. Sampling effort for each of the categories (mean net-h per net ± 1 SD) was: 16 "intact forest" nets (500.7 ± 28.3), 16 "gap" nets (477.6 ± 28.6), and 16 "mixed forest" nets (490.3 ± 25.1). Sampling efforts were different enough ($F = 2.86$, $P = 0.068$, one-way ANOVA) that analysis was performed upon capture rates, rather than individual captures.

Radio telemetry (2-g transmitters) was used to determine the home range size of 17 "sedentary" individuals using the La Peninsula site during the study period. Home range size was estimated using the modified minimum area method of Harvey and Barbour (1965). We did not sample all of the sedentary individuals occupying this site during these two winters in this manner. Further details on the telemetry aspect of this investigation can be found in Rappole et al. (1989) and Winker et al. (1990).

The La Peninsula site underwent very light selective logging in the mid-1970s. Vegetation occupying tree removal sites did not appear to be different in structure or composition from that occupying natural treefalls. All stumps on the La Peninsula site were located and mapped. The uneven distribution of stumps caused us to divide the site into two parts, one (3.5 ha) we called Part A (ca 1.1 stumps/ha), and the other (5.25 ha) Part B (ca 11.4 stumps/ha). The two parts were similar visually.

Rather than sample each net site, points for vegetation analysis were selected to ascertain the structure of forest used by thrushes whose home ranges were restricted to Part A or Part B. From radio tracking results no individuals appeared to use any of our qualitative microhabitat categories exclusively. Although our vegetation analysis considers the macrohabitat structure of different areas of forest rather than the structure of the specific microhabitat types sampled by individual nets, we think it is important to quantify the overall structure of forest used by Wood Thrushes rather than selectively quantify the extremes they encounter. The Santa Martha site was located in virgin forest at a higher altitude, and is included here for an "outside," macrohabitat comparison.

Vegetation analysis was conducted using a modified point-quarter method (Cottam and Curtis 1956, Phillips 1959). Plant taxonomy was ignored, and types were separated largely by size. Trees were defined as woody stems >7 cm diameter at breast height (dbh). "Saplings" were woody stems 2–7 cm dbh, and "shrubs" were plants both woody and non-woody from seedling size to 2 cm dbh. "Saplings" were mostly understory palms, primarily *Astrocaryum* species. "Shrubs" were primarily young "sapling" species and plants whose adult sizes fell between that of saplings and common herbaceous species. Canopy and ground cover were estimated as outlined by James and Shugart (1970). Because lianas (woody vines) and true vines are an important element of the tropical forest (Gradwohl and Greenberg 1980), they were counted when present on any tree or sapling measured, and each was categorized on the basis of diameter (by increments of 0.5 cm). Younger aerial roots of hemiepiphytes (e.g., strangler figs) close to tree trunks were probably measured occasionally, although when distinguishable (usually due to their stage of growth) they were excluded. Fifty points were sampled at Santa Martha and from both parts of the La Peninsula site (150 total); sample points were selected at random from the 25-m grid points. See Winker (1989) for more details of methods and descriptions of study sites. Overall netting effort was as follows: La Peninsula: 48 nets, 23,498 net-h; Santa Martha: 16 nets, 832 net-h.

Results.—We captured 117 Wood Thrushes on the La Peninsula site during the winter periods considered; because of statistical assumptions of independence, recaptures are not included in this analysis. Capture rates were normal in distribution (Kolmogorov-Smirnov test). To satisfy the assumptions of the statistical test, analysis was performed upon log-transformed capture rates ($\log_{10}$[1 + capture rate of net x]). Capture rates of Wood Thrushes were higher in nets sampling "gap" sites (8.52/1000 net-h, SD = 6.74) than in "intact forest" (3.14/1000 net-h, SD = 2.52) and "mixed forest" nets (3.55/1000 net-h, SD = 3.25; F = 6.5, P = 0.003, one-way ANOVA). This suggests within-forest, or microhabitat preference.

Home range sizes on the La Peninsula were as follows: Part A (N = 6) $\bar{x}$ = 0.64 (±0.31) ha; Part B (N = 11) $\bar{x}$ = 0.30 (±0.11) ha; overall (N = 17) $\bar{x}$ = 0.42 (±0.26) ha. Home ranges were significantly larger within Part A of the La Peninsula site than in Part B (t = 4.48, df = 14, $P < 0.001$; t-test for independent samples, unequal variance).

Forest structure among the three sites differed in several respects (Table 1). Part B had significantly smaller trees on average ($\bar{x}$ = 0.23 m dbh) than Part A ($\bar{x}$ = 0.32 m dbh) and Santa Martha ($\bar{x}$ = 0.32 m dbh; χ^2 = 13.12, P = 0.001, Kruskal-Wallis). This analysis is presented with the caveat that such a comparison suffers from Hurlbert's (1984) pseudoreplication. Lack of replication, as well as several differences between these plots (e.g., topography, altitude) result in an inability to ascribe any of the similarities or differences found to a single causative factor. Nevertheless, it appears that on Parts A and B, differences in ground cover (apparently negatively correlated with canopy cover) correspond with the differences found in home range size on the two parts (Table 1).

On the Santa Martha site only one Wood Thrush was captured, and at most only one individual was seen on any given day (the marked individual following capture). This capture rate was lower than the capture rate on either Part A or Part B of the La Peninsula site (χ^2

TABLE 1

VEGETATIVE STRUCTURE OF THE LA PENINSULA AND SANTA MARTHA SITES. PART A AND PART B ARE SUB-PARTS OF THE LA PENINSULA SITE

	Part A	Part B	Santa Martha	ANOVA[a]
Trees/ha	528 (319, 1036)[b]	616 (327, 1570)	373 (217, 783)	(A, B)(SM)
Basal area (m^2/ha)	42.9 (11.1, 95.4)	24.7 (7.3, 52.2)	29.3 (3.3, 81.10)	
Ground cover (%)	39.6 (23.2, 56.0)	70.0 (57.6, 82.4)	39.4 (26.5, 52.3)	(A, SM)(B)
Canopy cover (%)	84.7 (75.5, 93.9)	61.7 (49.3, 74.1)	84.1 (71.1, 97.1)	(A, SM)(B)
"Saplings"/ha	2783 (1543, 6443)	2609 (1425, 6235)	2296 (897, 14,349)	(A, B, SM)
Seedlings/ha	13,146 (6012, 48,374)	23,729 (10,525, 95,472)	18,159 (5535, 509,744)	(A)(B, SM)
Canopy height (m)	18.3 (11.3, 25.3)	13.4 (6.8, 20.0)	22.2 (13.1, 31.3)	(A)(B)(SM)
Mean diam. lianas/stem (cm)	3.6 (1.0, 6.2)	2.4 (0.6, 4.2)	1.5 (0, 3.2)	(A, B)(SM)

[a] Results of one-way ANOVA performed upon raw measurement data. Groups within parentheses do not differ significantly. A = Part A, B = Part B, SM = Santa Martha, parenthetical groups differ significantly ($P < 0.05$).

[b] Because some mean values represent estimates calculated with a formula involving distance squared, parenthetical values represent a range calculated from the mean ± 1 SD.

= 23.0, $P < 0.00005$, Kruskal-Wallis) suggesting that this area was marginal for the species—possibly due to altitudinal differences (150 m vs 470 m). Given several structural similarities between the Santa Martha site and the La Peninsula site (particularly ground and canopy cover, Table 1), vegetative characters alone do not appear to be predictors of thrush distribution in Los Tuxtlas.

Discussion.—Broad descriptions of "habitat preference" provide only a very coarse-grained assessment of a bird's needs. Although many migrants are known to prefer various forest types on their wintering ranges (Rappole et al. 1983), little is known of settlement and movement patterns within these forests. At La Peninsula, capture rates suggest that within this lowland rainforest Wood Thrushes preferred areas with gaps. Sedentary birds bearing radio transmitters had smaller home ranges in an area with heavier ground cover than elsewhere on the study site. Capture rate differences between our qualitative microhabitat types may simply reflect that nonterritorial birds frequent such areas. The Wood Thrush is primarily a ground-level forager, though, and the heavier ground cover found in Part B (which implies higher ground-level production) suggests that such areas would be preferred foraging locales for sedentaries as well. Territory size is often inversely correlated with food density (Featherstone 1966, Watson 1967, Cody and Cody 1972, Gill and Wolf 1975). Smaller average home range size in Part B of the La Peninsula site is consistent with the hypothesis that heavier ground cover within forest has a positive value to sedentary Wood Thrushes.

Denser understory within the forest can be caused by any factor creating canopy breaks. On our site these included treefalls, stream passage, and steep slopes, but river passage and soil type might be additional contributing factors elsewhere. The apparently even distribution of territorial birds in the forest (Rappole and Warner 1980:360–61, Winker 1989), together with observations of individuals whose home ranges included no gaps, shows that this type of microhabitat is not required.

Although it appears that gaps are used more frequently by Wood Thrushes than areas of relatively open understory, this increased use is not immediately apparent. The selective logging done on our site in the mid-1970s artificially raised the number of treefalls on Part B, and enabled us to know the relative age of most of our gap understory microhabitats (ca 10 yr). No thrushes were seen frequenting recent treefall sites (2–3 yr old) in the forest, other than occasional edge use (pers. obs.). Webb et al. (1977) found that the Wood Thrush showed declines following 100% logging (clearcutting) on its breeding grounds in the Adirondacks. During the 10 years after clearcutting, the species increased until populations were at or above pre-logged levels. Our data suggesting heavier use of gaps, most nearly 10 yr old, combined with observations showing little use of areas recently disturbed (2–3 yr old) imply that increased use of gaps by Wood Thrushes occurs only after years have passed, and is probably related to development of understory vegetation. Study of the effects of selective logging on other species would be necessary before advocating such a management practice for tropical forests (for example, see Crawford et al. 1981). Selective logging in Los Tuxtlas has usually been a precursor to total forest eradication (pers. obs.). If the La Peninsula site had not been located within a recently protected area (Reserva Biosfera de la Sierra Santa Martha), it is questionable whether any forest would have remained for a 10 yr period following logging.

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Boat census of Bald Eagles during the breeding season.—Subadults, birds in predefinitive plumage, and non-breeding adult Bald Eagles (*Haliaeetus leucocephalus*) are poorly censused by breeding season aerial surveys (Whitfield et al. 1974). This study tests whether a boat survey provides a reliable estimate of the number of individuals in a summer (May–August) population of Bald Eagles on a moderately large lake. Boats have been used to locate nests (Hodges 1982, Gerrard et al. 1983), but should also be suitable for counting eagles since these birds spend much time at the aquatic-terrestrial interface (Leighton et al. 1979, Gerrard et al. 1980, Gerrard and Bortolotti 1988). A second objective was to test whether eagle numbers fluctuated in response to the availability of dead fish. Preliminary studies showed occasional congregations of immatures and non-breeding adults on small lakes adjacent to Besnard Lake; we censused such lakes to achieve a third objective—to find out whether changes in the population on Besnard Lake resulted from movements to and from these nearby lakes.

Study area and methods.—Besnard Lake (55°25′N, 106°00′W) lies along the southern boundary of the Canadian Shield region in north-central Saskatchewan. The lake has an irregular outline with rocky shores and numerous islands. The shoreline length is 400 km (as measured using 1:15,000 scale maps) with a surface area of 197 km^2, of which 177 km^2 is open water and the remainder is occupied by 255 islands (Chen 1974). It is surrounded by low, forested hills, not exceeding 100 m in height. White spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) predominate near the lake shore. The study area also includes six small lakes of 0.4 to 3.7 km^2 water area near Besnard Lake. The character of the shores and forests surrounding these lakes was similar to Besnard Lake, except that one of the small lakes had extensive shallow, reedy areas. Eagles breeding on these lakes were not significantly affected by DDT, and the population has been stable from 1973 to 1989 (Gerrard et al. 1983, Gerrard 1985).

Bald Eagle surveys.—Twenty-three boat censuses of Besnard Lake were conducted; nine in 1976, eight in 1977, two in 1978 and four in 1984. At least one census was conducted per month from May to August each year, except for 1978 when the July and August censuses were omitted. The design of the boat census was based on an earlier raptor census by Craighead and Craighead (1969). The shoreline was divided into 50 sections of 8 km each. To reduce the total time of the census, each census consisted of a survey of half of the shoreline of the lake; a pilot census in 1975 showed that surveying fewer than half the sections reduced the accuracy of the overall census. Alternate sections (i.e., 25 sections total) around the lake were censused by one or more observers traveling 100 m from shore in a motorized canoe or other boat at a speed of 8–16 km/h. If an eagle was flushed, it tended to fly into the next section (i.e., one that was not on the present census) thus reducing the likelihood of counting any eagles twice. Censuses were conducted during daylight hours when winds were less than 32 km/h and visibility was good. No censusing was done in moderate or heavy rain. A complete census of 25 sections took three to eight days ($\bar{x} = 4.8$), depending on the weather.

TABLE 1
AVERAGE NUMBER OF EAGLES PER SECTION 1976–1978

	Sections with active nests (147)[a]	Sections with empty-occupied nests (66)	Other sections (262)
Adults	1.65	1.64	0.50[b]
Subadults	0.41[c]	0.80	0.65

[a] Number of such sections surveyed.
[b] $\chi^2 = 78$, $P < 0.001$ that the number of adults in other sections is lower than that in sections with nests.
[c] $\chi^2 = 7.0$, $P < 0.01$ that the number of subadults in sections with active nests is lower than that in all the remaining sections.

Census sections were divided into those with an active nest (a nest with incubating adult or young present), those with an empty-occupied nest (those containing a nest attended by a pair of adults but with neither eggs nor young at the time of the census), and other sections (see Gerrard et al. 1983). The status of each nest or breeding area was monitored during the summer, both during the surveys and by additional visits. For the population estimate we used a stratified sampling approach with two strata based on the relative distribution of adults and immatures (Table 1). For adults, the lake was stratified into sections with occupied nests (those with active and empty-occupied nests combined) and other sections. For immatures, the lake was stratified into sections with active nests and all other sections (i.e., empty-occupied and other sections).

"Adult" eagles have white heads and tails. Birds with minute brown spots on the head and tail (the Basic IV plumage; Palmer and Gerrard 1988, McCullough 1989) were also included in this category, but birds with a stripe through the eye, brown crown or brown terminal band on the tail were excluded (Basic III plumage; Palmer and Gerrard 1988, McCullough 1989). Five nestlings marked on Besnard Lake and resighted when four years of age all had adult plumage. Thus, adults are presumed to be four years of age or older. The term "immature" is used to include all other younger eagles, and by comparison with known-age birds marked on the lake (Gerrard et al. 1978) were one, two, or three years old at the time of the census. A hatching-year bird was an eagle raised in the year of the census. No hatching-year birds fledged before the last two days in July and most were in the nest until mid-August. Except where specifically noted, hatching-year birds, readily identified by plumage and behavior, were excluded from counts of immatures for the purpose of the census.

The shorelines of six small lakes near Besnard Lake were surveyed during 1976 and 1978. Ninety km of shoreline were searched during May and June and 120 km during July. To calculate eagle numbers using a Petersen estimate, and to monitor local movements, we used patagial tags to color mark 56 nestling eagles on Besnard Lake from 1973–1975 (Gerrard et al. 1978).

Fish survey.—Fish are the primary prey of eagles in our study area and are often captured injured or dead on the water surface (Gerrard and Bortolotti 1988). During the surveys in 1976 and 1977, one observer watched for dead or injured fish floating on the lake surface. Since the ability to see such fish varied with the height of the waves, the distance from the boat at which fish could be seen was estimated. The distance travelled was then multiplied by the visibility on each side of the boat to give an estimate of the area of lake surface scanned for fish.

Besnard Lake population.—There was a consistent trend for the number of eagles on

TABLE 2
RESULTS OF BESNARD LAKE BALD EAGLE CENSUSES 1976–1984

Month	No. of surveys	Estimated adult population No.	Estimated immature population No.	Estimated immature population %	Total population No.
May	6	49.4 ± 2.3*	20.1 ± 2.2[a]	29%	69.5 ± 1.1[a]
June	6	41.6 ± 2.0	20.7 ± 2.5	33%	62.6 ± 3.5
July	6	60.5 ± 3.5	45.0 ± 5.2	42.5%	105.8 ± 4.1
August	5	60.3 ± 2.1	31.1 ± 6.5	33.9%	91.8 ± 7.5

[a] Results are presented as the mean ± SE of the estimates from the individual surveys.

Besnard Lake to be lower in May and June and higher in July (Table 2). The number of adults present on the lake on all May and June censuses averaged 45.5 ± 1.9 ($\bar{x}$ ± SE, N = 12), while in July and August there was a significant increase ($P < 0.0001$, unpaired t-test) to a mean of 60.6 ± 2.1 adults (N = 11) (Fig. 1, Table 2). The number of immatures on the lake averaged 20.4 ± 1.6 (N = 12) on the May and June censuses, while it increased

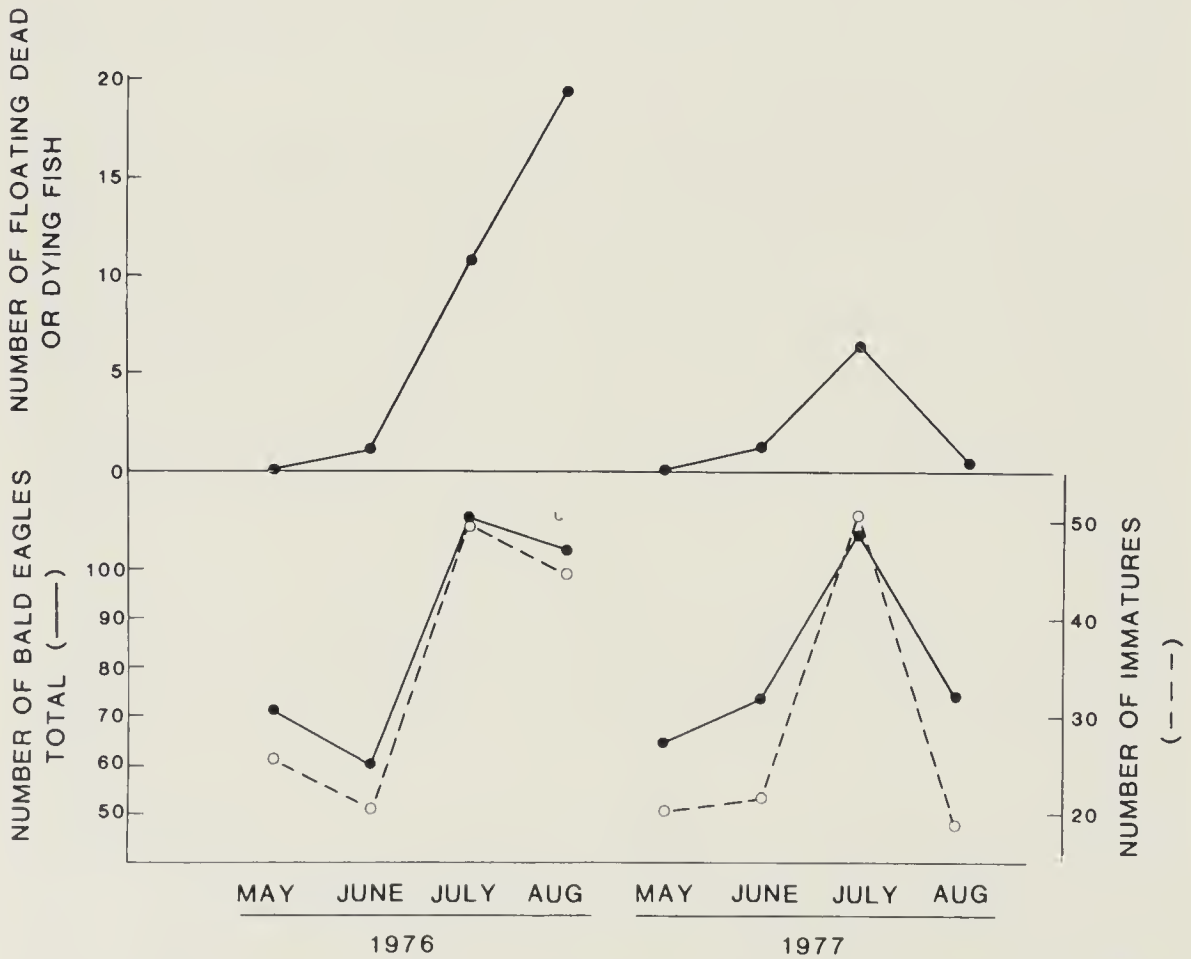

FIG. 1. Mean number of dead or dying floating fish per 10 km² lake surface. The number of Bald Eagles and the number of immatures on Besnard Lake are shown as the mean for all censuses in a given month.

($P < 0.005$) to an average of 45.0 ± 5.2 (N = 6) on the July censuses. In August of 1976, the number of immatures on the lake averaged 44.0, while in August, 1977, it declined to an average of 17.2.

When the number of fledglings ($\bar{x} = 27.8$ for the four years) is added to the number of adults and subadults on the lake, the average number of eagles on the lake in August was 119.5 which is 0.30 eagles/km shoreline or 0.68 eagles per km² water area.

Distribution of eagles.—All nests at Besnard Lake in 1976 to 1978 and in 1984 were within 200 m of the lake shore. Eagles were not distributed evenly along the shoreline. More adults were in sections with active or empty-occupied nests (Table 1). Immatures were less likely to be found in sections with active nests (Table 1). Immatures were less likely than expected to be found closer than 2.4 km to an active nest (mean 5.1 immatures/100 km in 875 km shoreline searched) and more likely to be found more than 2.4 km from an active nest (mean 10.1 immatures/100 km in 724 km searched) (Chi-square test, $\chi^2 = 12.1$, df = 2, $P < 0.01$). Our observations of territorial behavior on Besnard Lake, similar to those of Mattson (1974) and Swenson et al. (1986), showed that immatures are actively excluded from the region near an active nest but not from the region near an empty-occupied nest.

Immatures often exhibited clumped distributions (Table 3), and were not seen regularly in the same sections. To test if the immatures consistently occupied the same survey sectors, we made use of May to July surveys of odd numbered sectors done in 1976. We counted the number of absences of immatures over the five surveys in each sector. Assuming that the occurrence of one or more immatures in a given sector in a survey is independent of that in other surveys, we expected a binomial distribution. We calculated the binomial probabilities, with $P = 18.20/25 = 0.7280$, which is the average fraction of sectors having no immatures. A Kolmogorov-Smirnov test showed no significant departure of the observed frequencies from those expected ($D = 0.06$, $P > 0.2$).

Table 3

Mean, Variance (S^2) and Coefficient of Dispersion (CD) for the Numbers of Immatures per Sector, by Survey Number

Survey number	Date	For all sections			Sections without active nests
		$\bar{x}$	S^2	CD[a]	CD
1	May 24–June 1	0.44	0.923	2.18**	2.11**
2	May 24–June 1	0.52	1.093	2.10**	2.4**
3	June 5–8	0.28	0.210	0.75 ns	0.59 ns
4	June 18–25	0.52	0.843	1.62*	1.34 ns
5	June 18–25	0.40	0.500	1.25 ns	1.18 ns
6	July 5–10	0.80	2.830	3.53**	3.83**
7	July 19–23	1.04	3.870	3.72**	2.71**
8	Aug. 2–5	0.72	1.043	1.45 ns	1.56 ns
9	Aug. 16–20	1.00	1.500	1.50 ns	1.52 ns
All surveys					
Sections without active nests		0.71	1.51	2.13**	
Sections with active nests		0.46	1.25	2.72**	

[a] ns $P > 0.05$; * $0.05 > P > 0.01$; ** $P < 0.01$ (the significance of departure of the coefficient of dispersion from unity was tested using $\chi^2 [N - 1] = [N - 1]S^2/\bar{x}$).

TABLE 4

THE NUMBER OF TERRITORIES ON BESNARD LAKE DURING THE YEARS OF THE STUDY

Year	Number of territories			Number of young fledged
	Occupied	Active	Successful[a]	
1976	21	15	14	24
1977	22	20	18	29
1978	23	19	17	27
1984	24	23	18	31

[a] Successful territory was one where young were raised to fledging.

Population movements in response to prey availability.—There were few sightings of floating dead or injured fish on Besnard Lake during May and June 1976 and 1977 (Fig. 1). A considerable increase occurred in July of both years. In 1976, numbers of fish continued to be high throughout August, while in August 1977 the number of fish declined to low levels. Using data from each census, there was a significant correlation between the number of floating dead fish per km^2 water surface and the lake population of immatures (Pearson product moment correlation $r = .67$, df = 15, $P = 0.009$), of adults ($r = .58$, df = 15, $P = 0.03$) and of all eagles ($r = .70$, df = 15, $P = 0.005$).

Population size on small lakes.—Surveys of several small lakes adjacent to Besnard Lake in 1976 and 1978 showed no active breeding areas but an eagle density in May and June (0.50 eagles/km shoreline) which was much higher than the May and June density of eagles on Besnard Lake (0.17 eagles/km shoreline). In July, the density of eagles along small lakes (0.22 eagles/km shoreline) was similar to that on Besnard Lake (0.27 eagles/km shoreline).

The results of the census show a considerable influx of immature and non-breeding adults onto Besnard Lake each year in July. The influx was associated with an increase in the availability of dead fish floating on the lake surface. The precise cause of the fish die-off has not been established, but may result from an increase in water temperature and a decrease in the dissolved oxygen. Observations in 1970 suggested there might be congregations of immatures at small lakes adjacent to Besnard at a time when white sucker (*Catostomus commersoni*), northern pike (*Esox lucius*), and walleye (*Stizostedion vitreum*) spawn in streams feeding from these lakes into Besnard Lake. The results of the present study showed an increase in the numbers of immatures and non-breeding adults using these small bodies

TABLE 5

SIGHTINGS OF MARKED SUBADULTS DURING 1977

Date	No. of marked birds seen	No. of birds seen well enough to see markers	Percent marked
July 1–15	2	29	6.9%
July 16–31	10	107	9.3%
Aug. 1–Sept. 15	4	49	8.2%
Total period	16	185	8.13 ± 0.69[a]

[a] $\bar{x} \pm$ SE.

of water during spawning in May and June and a decrease in July and August and they are consistent with a movement of eagles from the small lakes to Besnard Lake at the end of June. Observations of two color-marked birds confirmed such a movement. A similar seasonal pattern has been suggested to occur in Minnesota (Fraser et al. 1985).

Accuracy and reproducibility of censuses.—Several observations suggest that the survey provided an accurate and reproducible estimate of the number of eagles around Besnard Lake. First, based on results from three occasions when two lake surveys were done simultaneously, the coefficient of variation for the number of adults seen on a single survey was 12.2%, for the number of immatures 8.4% and for the total eagle population 4.3%. Second, in May and June, adults not associated with nests were virtually absent from Besnard Lake. The number of adults seen on the surveys was close to a predicted value of two times the number of occupied breeding areas on the lake (Table 4). For 1976 the mean number of adults on the May and June surveys was 40.6, while the expected was 42. For 1977 the comparable numbers were 47.9 and 44, for 1978 they were 49.5 and 46, and for 1984 they were 47.4 and 48. Third, sightings of color-marked birds showed that resighting of individuals on a given survey was rare. Of 23 color-marked birds seen on the censuses, only one was seen twice on the same census.

Fourth, in 1977, during one sixteen-day period, 107 immatures were seen well enough to tell whether color markers were present. Ten of these birds were marked and represent a minimum of four individuals. Based on these sightings and on a mean of 8.13 ± 0.69% ($\bar{x}$ ± SEM) of birds on the lake being marked (Table 5), a Petersen estimate can be used to calculate a minimum of 49.2 (45.4–53.8) subadults on the lake during this period. Three of the marked eagles sighted were from a small group which were "batch" marked with similar colors. If these are counted as unmarked to reduce the uncertainty of whether these sightings represented one or more birds, then there were in the 107 sightings, seven marked sightings of three different birds. This information, under assumptions similar to that of the Petersen method is sufficient to form a maximum likelihood estimate of the subadult population. This method was worked out by Arnason et al. (unpubl. data), and gives a most likely estimate of 46. These figures can be compared to results of two censuses done during this period which estimated a lake population of 48 and 54 subadults respectively.

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Male Eastern Bluebird rears four broods during one nesting season.—The Eastern Bluebird (*Sialia sialis*) is multi-brooded and rears either two or three broods over most of its range. Peakall (1970) found that: (1) two broods are reared in most of the range, (2) three broods are common in the central portion of the range, and (3) one brood is most common in Canada. Although four clutches of eggs have been reported (Laskey 1943, Thomas 1946), the maximum number of successful broods to be reported is three. This paper reports a male Eastern Bluebird that apparently reared four broods during the 1987 nesting season by alternately mating with two females.

The study area consisted of an improved pasture located in Cullman County, Alabama. Nest-boxes were equipped with shutter-traps (Fischer 1944) and placed along fencerows.

Adult Bluebirds were banded with U.S. Fish and Wildlife Service aluminum bands. Observations of nesting bluebirds were limited to one or two visits per week to check nest contents and to one trapping session per nest. A trapping session consisted of 1–2 h of observing a nest-box until both members of a presumed pair (i.e., one adult of each sex) were trapped upon entering the box to feed nestlings. During the trapping sessions, no more than one bluebird of each sex was observed in the area containing the nest-boxes, and it is, therefore, assumed that the adults trapped at a nest were a mated pair.

On 31 May 1987, a male Eastern Bluebird, previously banded as a nestling 26 July 1986, was trapped in nest-box #9 after entering to feed the two-day-old brood of an unbanded female who was trapped and banded at that time. A nest containing one egg was located 163.5 m away in box #6 on that day. On 24 June 1987, the male was trapped in box #6, while caring for the second brood with another unbanded female who also was trapped and banded. On 18 July 1987, the male was trapped at the third nest after entering box #8 (located 98.1 m from box #6) to feed the two-day-old brood of the original mate. The male was trapped again with the second female at box #6 on 12 August 1987 while caring for a three-day-old brood. All four broods successfully produced fledglings (N = 5, 5, 3, and 3, respectively).

Eastern Bluebirds exhibit a predominately monogamous mating system (Gowaty 1981); therefore, most nesting reports have been based on monogamously paired birds. Polygyny has been reported (Pontius 1928, Gowaty 1983); however, literature documentation is limited. Although the observations described here suggest a polygynous relationship, that conclusion may not be warranted. For example, even at nests with color-banded individuals and more intensive observations than these, Gowaty and Karlin (1984) found that patterns of parental care did not necessarily reflect genetic kinship between putative parents and offspring. In addition, adult male Eastern Bluebirds have been documented to act as helpers (Pinkowski 1975) and to adopt (Pinkowski 1978). The observations reported here may not have been extensive enough to ascertain the actual relationship between the male and his apparent mates and nestlings. However, the observation of an adult male Eastern Bluebird participating in rearing four broods in one nesting season is unique and contributes to our knowledge of the wide range of variability found in the complex mating systems of the species.

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A group of young Peregrine Falcons prey on migrating bats.—Although Peregrine Falcons (*Falco peregrinus*) hunt primarily avian prey, they have been known to kill and eat bats when the opportunity arises (e.g., Stager 1941, Sprunt 1951, Sick 1961, Baker 1962, Albuquerque 1978, Pierson and Donahue 1983, Sherrod 1983:59, Palmer 1988). Most observations have been made in southern regions, chiefly in the southern hemisphere, and usually involve Peregrines taking advantage of easily obtainable prey where large concentrations of bats gather at dawn and dusk. Few detailed observations of Peregrine bat-hunting behavior have been published however, especially for Peregrines in the northern United States.

On the mornings of 30 August, 2 September and 10 September 1989, five juvenile Peregrine Falcons which had been recently released from a hacking tower near Lake Michigan in northeastern Illinois, were observed preying upon three species of migrating bats (silver-haired, *Lasionycteris noctivagans*; big brown, *Eptesicus fuscus*; and red, *Lasiurus borealis*). The falcons, observed daily from dawn until dark during the entire summer and fall, killed many bats on all three mornings when the bats, migrating across Lake Michigan, did not reach the cover of the Illinois shoreline before daybreak. Twenty-eight kills were seen over the three days, and indirect evidence of at least 15 more kills was found. Skies were clear to partly cloudy with gentle north-northeast winds (2–9 km/h) on all three days, and temperatures were mild (21°–25°C). Most kills took place between 06:00 and 10:30 CST.

The falcons were still learning to hunt and had made their first kills only two weeks or so previously (large insects and small passerines). When hunting for bats, the falcons scanned the horizon over the lake while perched on boulders, cement breakwaters, dead trees, or tall utility poles. The falcons were usually within 10–30 m of the water's edge, and at intervals of 2–100 m from each other. Bats migrated in a south-southwest direction across Lake Michigan, and during peak arrival times appeared at a rate of approximately 1/min. They usually flew 10–30 m above the water's surface, and arrived singly or in groups of only two to four at a time rather than in dense flocks. Their irregular flight and distinctive fluttery wingbeat made them easy to distinguish against the horizon. Kills usually took place as follows. One or more falcons would fly out over the water in fast, direct flight to intercept an approaching bat. Most bats were intercepted 50–100 m from shore, although some were caught much farther away and some were not caught until they reached land. The first falcon to fly out after a bat was followed immediately by two to four of the others, and all would quickly but silently converge on the prey. Upon reaching the prey, the falcons became vocal, emitting playful screams (Sherrod 1983:189) as they extended their talons and began an erratic attack, diving and swooping at the bat. They did not stoop at the bat from great

heights, but rather tried to follow it closely, making shallow dives and braking with their wings, while grabbing at the bat whenever possible, and from every conceivable angle, sometimes almost colliding with one another in the process. The bat invariably began a series of evasive actions as it tried to avoid capture. Within 15–35 sec, or in approximately four to eight attempts, one of the falcons usually succeeded in capturing the bat with its talons. The falcon would then fly directly back to a perch to eat the bat, often pursued by two or three of the other, now very vocal young falcons, which emitted food-begging screams (Sherrod 1983:185) as they followed. At no time did any of the falcons attempt to eat their catch while still on the wing, although they did, on several occasions, deliver a single bite to the bat right after catching it. After landing on a perch the falcon would either eat the bat in its entirety in four or five large chunks, or it would eat the meat and membranes only, delicately biting off small pieces and leaving a nearly intact skeleton behind.

Most of the kills observed involved at least two, and usually three or more falcons pursuing and surrounding a single bat, even when there were several other bats flying nearby, as was usually the case. This behavior, while social in nature, probably should not be viewed as cooperative hunting, but rather as the "close-focused," hit-or-miss behavior that might be expected in a group of young, inexperienced Peregrine Falcons still developing their hunting skills (Sherrod 1983:49–63).

Falcons were twice observed forcing bats down into the lake and subsequently, after several attempts, plucking them up from the surface (once close to shore in 5 cm of water, and once approximately 50 m off-shore, where the water was approximately 5 m deep). On another occasion, a falcon pursued a bat shoreward and then followed the bat in an "Accipiter-like" manner, into a dense stand of cottonwood trees (*Populus deltoides*). The outcome could not be seen.

Bats that reached land quickly dropped into any available cover, or even onto bare ground, where they remained completely motionless (even allowing humans to pick them up). The falcons were never seen picking up a bat that had dropped to the ground; they usually gave up the chase immediately in such cases, without trying to flush the prey back into flight, and returned to the beach to renew the hunt. The selective nature of the hunt was obvious. During periods when bats were arriving, a time span of about four hours on each of the three days, the falcons focused their attention almost exclusively on searching for bats. Even a time lag of 15–20 min between bat sightings did not cause the falcons to pursue the many other types of prey which were in the immediate vicinity. Only after 30–40 min of unproductive waiting would the falcons begin to hunt elsewhere or for other prey.

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ORNITHOLOGICAL LITERATURE

CURRENT ORNITHOLOGY. Volume 6. Edited by Dennis M. Power. Plenum Press, New York. 1989:332 pp. $59.50.—This volume is the first under the editorship of Dennis Power, who states that the purposes of the series are: (1) to provide information to researchers needing concise overviews, (2) to provide updates on specific schools of thought, and (3) to stimulate and suggest directions for new research. By my reckoning, three chapters fall in the first category, two fall in the third category, but one chapter does not fit into any category and travels out of the realm of ornithology and science.

The three review chapters all deal with migration. First, Kerlinger and Moore demonstrate how atmospheric structure should affect bird migration, based on wind patterns and changes in relative humidity and temperature. The results that birds using flapping flight should migrate at night and soaring birds should migrate during day seem straight forward if atmospheric structure is the selective force that they contend. Next, Lövei discusses migration of passerines between the Palaearctic and Africa, where, unlike New World migrants, birds migrating to Africa cross many geographical barriers, including water, mountains, and the Sahara Desert. Many are fruit eaters during migration, and many species have a "step" migration pattern, visiting a series of areas during each winter as resource abundances change. Lövei ends his chapter on a cautionary note: habitat destruction on wintering grounds and at migratory stop-over areas and increasing spread of deserts may have profound adverse effects on Palaearctic migrants. Indeed, certain species that winter south of the Sahara have already begun to decline in numbers, in a manner similar to the decline of some passerines in the New World. Lastly, Waldvogel presents the opinion of the Cornell research group: "claims that olfaction forms a universal and essential element of pigeon homing must be considered unsubstantiated at this time." Two research groups, one in Italy and one in Germany, contend olfaction is important in migration, while two groups, one at Cornell and one in Germany, contend that it is not. I cannot foresee how this conundrum is going to be resolved very easily. As Waldvogel remarks, however, we know a lot more about avian olfaction than we did prior to this controversy.

The first two chapters are the most stimulating. Breitwisch contends that breeding bird populations do not have a 50-50 sex ratio, but a sex ratio in favor of males, and that females suffer greater mortality between fledging and their first breeding attempt. Brashly contending that that is so, he reviews the various reasons why more fledged females die than males. That leads to a reexamination of the argument that fewer females are found in breeding populations because they make more of a parental investment (PI) in young than do males. Breitwisch concludes that little data exist to argue that male and female PIs differ in bird populations. There are, however, a few problems with this chapter. For one, much of what he contends is based on very few data. Secondly, although problems with quantifying PI are mentioned, few insights are offered about how to overcome those problems, particularly in terms of measuring "risk." For example, he takes a hard line on female disappearance during brooding and incubation: only actual cases of predation can be used and those need to be compared with predation rates on roosting males. Since much of that occurs at night, and who knows where males are roosting, this is no easy task. Nonetheless, Breitwisch's chapter should interest anyone conducting research on avian breeding ecology and much of what he contends lends itself to testable hypotheses. Only time and more data will tell if he is right, or out in right field.

Butcher and Rohwer address conspicuous and distinctive coloration in birds, which they term "colorfulness." If colorfulness acts as a signal, they contend that we should be able to discover what a bird is trying to signal about. They review all proposed hypotheses covering

a wide variety of reasons, in an attempt to explain the "three rules of avian color dimorphism": (1) males tend to be more colorful than females, (2) adults tend to be more colorful than young birds, and (3) breeding season birds tend to be more colorful than nonbreeding season birds. The general conclusions are that some form of sexual selection is important in maintaining colorfulness, that no one reason is likely to explain a wide variety of color patterns, and that there could be multiple reasons for a specific color pattern. Butcher and Rohwer mention ways to test various hypotheses, so that this chapter would be useful to anyone wishing to investigate color patterns in birds.

The most interesting and controversial chapter is by Noel and Helen Snyder on the California Condor (*Gymnogyps californianus*). Occupying nearly a third of the volume, the Snyders present a biased account of events leading to removal of condors from the wild. They are up-front about that, however, stating that they are not trying to please people, but rather to present their own personal assessment of the biology and conservation of condors. In so doing, they name names, point fingers (sometimes at themselves), and offer their candid opinions concerning why certain individuals and agencies acted in certain situations. I suspect that many people are not going to be happy with this chapter.

The Snyders start by reviewing the history of research on condors. Koford's research (late 1930s and 1940s) is discussed in detail, as is a follow-up study by his friends, the McMillan brothers (early 1960s), published with Alden Miller. A main point of controversy is Koford's estimate of 60 condors, which the Snyders (and others) conclude was a gross underestimate of possibly 120 to 180 birds, and the McMillans' estimate of 40 condors some twenty years later, which the Snyders conclude was also an underestimate of 80 to 120 birds. During the 1960s and 1970s, systematic censusing of condors began, and estimates of about 60 birds were made in the late 1960s. More controversy arose since those who believed Koford's estimate contended that condors were holding their own, while others believed that condors were in decline. The McMillans, of course, argued that censuses were over-estimating condor numbers. By 1980, however, nearly everyone agreed that condors were in decline and that serious steps needed to be taken. Despite nearly 40 years of research, the Snyders contend that we entered the 1980s with little information concerning causes of the decline.

In 1981 the Condor Research Center was established in California, funded by a variety of government and private organizations. This coincided with a major breakthrough in censusing when it was realized that individual condors could be identified by photographs. Photocensusing revealed the grim truth at last: the number of condors seen each year between 1982 and 1985 was 21, 19, 15, and 9, respectively. Based on their research in the 1980s, the Snyders conclude that excessive mortality, due to wanton shooting, lead poisoning from ingestion of bullets (not lead shot), and possibly collisions with powerlines, was responsible for the rapid decline. The Snyders further state that habitat preservation, which had been the focus of conservation efforts since the 1940s, was the least pressing problem in the short term, although it is important in the long term.

The Snyders next turn to the "quagmire" of condor conservation. Extensive controversies arise when dealing with sketchy data and big egos, and when research careers are on the line, and the Snyders present all the dirt leading up to the suggestion in 1985 that all remaining nine condors be placed in captivity. According to the Snyders, all logic seemed to break down at this point. The United States Fish and Wildlife Service (USFWS) is placed in a very bad light, as is the National Audubon Society (NAS), which is portrayed as hindering many efforts of the Condor Recovery Team. Even the American Ornithologists' Union's Condor Committee made a contradictory recommendation that all birds should be captured, but that a few should be left in the wild to help preservation and research efforts. The Snyders contend that acquisition of the Hudson Ranch, a 50-km^2 grassland now known as Bitter Creek National Wildlife Refuge, as a place to release condors was also a fiasco. Although

they themselves initially backed the NAS plan for this refuge, later research led them to believe that this is one of the last places where condors should be released.

In a final discussion section, the Snyders give a retrospective view of the condor problem, given their feelings that condors were once doomed to extinction in the wild and that the captive breeding program has the potential to some day return condors to the wild. Here they make their most damning statements: based on conversations with administrators, they "learned" that decisions by both the USFWS and NAS were driven by short-term self-interests and the need for program preservation, rather than an objective interest in saving the condors. (I talked with a high-ranking administrator from one of those organizations recently who thought that the Snyders' remarks were patently false.)

What is this exposé doing in "Current Ornithology"? Ironically it reads more like an article out of NAS's own magazine, *Audubon.* The Snyders contend that the public spent a lot of money on condors and they need to know from people involved what really happened, but what percent of the American public reads "Current Ornithology"? Editor Power states that the chapter "reveal[s] the fascinating undercurrent of politics and interactions driving the development of decisions affecting endangered species." How does this fit the stated objectives of the series? I surmise this is a new editorial tack to make "Current Ornithology" more "current" through controversy which certainly makes exciting reading. Power asks for readers' comments and criticisms. I suspect he will get some concerning this chapter.—KIMBERLY G. SMITH.

RARE BIRDS IN BRITAIN AND IRELAND. By J. N. Dymond, P. A. Fraser, and S. J. M. Gantlett. T. & A. D. Poyser, Ltd., Staffordshire, England, and Buteo Books, Vermillion, South Dakota. 1989:366 pp., county map, species distribution maps, seasonal occurrence bar graphs, line drawings of birds (by many artists). $55.00.—This book is a successor to two previous works of the same genre, the second of which even bears the same title: "Scarce Migrant Birds in Britain and Ireland" (1974) by J. T. R. Sharrock, which covered "records of some two dozen species of regularly occurring rarities and rare migrants between 1958 and 1967"; and "Rare Birds in Britain and Ireland" (1976) by J. T. R. and E. M. Sharrock, which "covered nearly all those species which, during 1958–1972, were considered by the *British Birds* Rarities Committee; it also included notable records of extreme rarities up until 1975." Neither of these books was reviewed in *The Wilson Bulletin.*

In the latest version, the authors "have analysed all published records for each species during the period 1958–1985; in addition, records of extreme rarities prior to, and subsequent to, this period have been listed."

These books should not be confused with another publication edited by J. T. R. Sharrock and published by Poyser in 1982, "Birds New to Britain and Ireland." That book consisted of reprinted and edited accounts from the journal *British Birds* of first (and a few second) occurrences of bird species in the British Isles, including photographs when these were available.

For each of the species in the present book, the English and scientific names are followed by a summary of the normal breeding and wintering range. A brief field-oriented description follows, usually stressing comparisons with more familiar British species. Each species is provided with a vignette line (or sometimes scratchboard) drawing, by one of 14 artists. For most species there are either one or two maps—the division is by season of occurrence—with a spot in each county (*not* for each locality) for which records have been accepted. The number of individual records per county is indicated by the size of the spot as shown on an accompanying key. The maps include only records through 1985, although some later ones are listed in the text.

Format for the discussion of the species' status depends on the number of records, with a full list for the rarest birds, a partial list (usually the 1958–1985 records) for others, and a general statement for more frequently occurring species. Older records may be mentioned in passing or fully listed (as, for example, are all records for the Eskimo Curlew [*Numenius borealis*]).

Except for species with five or fewer records, one of two kinds of bar graphs is presented. The vertical axis for all of these is numbers of records; the horizontal axis is divided into months of occurrence (subdivided into four periods) for some species and years 1958–1985 of occurrence for others.

Additional remarks vary in size and scope from none to brief comments on geographic and/or seasonal trends.

Illustrations are not really necessary for a book of this kind, but they undeniably add to its attractiveness. As is true of several books published in Britain in recent years, the dust jacket bears the only color illustrations, in this case a Wallcreeper (*Tichodroma muraria*) on the front and an autumn American Robin (*Turdus migratorius*) on the spine. The artists cannot be blamed for failing to capture the *Gestalt* of North American birds with which they are unfamiliar, such as the Philadelphia Vireo (*Vireo philadelphicus*), several of the Parulinae, and the Fox Sparrow (*Passerella iliaca*). Oddly, the authors place the latter species in *Zonotrichia* while retaining *Melospiza* for the Song Sparrow, although the Fox Sparrow is the most distinctive species in the *Melospiza-Zonotrichia-Passerella* complex.

David Parkin (B[ritish] T[rust for] O[rnithology] News No. 165:8, 1989) has criticized this publication from the viewpoint of a contemporary observer of British birds, expressing his keen disappointment that the book is merely an update rather than a true revision. He states that criticisms of the earlier versions were not addressed in the new one, and that the book suffers particularly from a lack of serious attempt to analyze the data. Some of the questions he suggests for further study include possible associations between arrival patterns of scarce Siberian and American birds, differences between adults and "juveniles," possible correlations between breeding success in Canada and vagrancy in Britain, etc. The database of occurrences is available on computer, and I fully agree with Mr. Parkin that an opportunity has been missed to go well beyond the mere listing of records. With the intensive interest in their avifauna that has always characterized the British, I do not doubt that an appropriate analysis of these records will eventually be forthcoming.—KENNETH C. PARKES.

BIRDS IN IRELAND. By Clive D. Hutchinson. T.^& A. D. Poyser, Carlton, England, and Buteo Books, Vermillion South Dakota. 1989: 215 pp., 13 black-and-white photographs, 100 drawings, 25 maps, 65 histograms, 62 tables. $55.00.—This literate and authoritative book was published to coincide with the twenty-first anniversary of the Irish Wildbird Conservancy. The book describes the status of the 397 species occurring in Ireland and 153 species recorded breeding in Ireland to the end of 1986.

The text is divided into sections covering introduction, acknowledgments, factors affecting the distribution of birds, ornithology and bird conservation, recent changes in status, background to the species accounts, the species accounts, appendices, list of local reports, principal organizations, scientific names of mammals, fishes and plants in the text, bibliography, general index, and species index.

The introductory chapters in 37 pages give a very useful overview of Irish habitat types, climate, location and other factors affecting distribution plus the history of Irish ornithology and conservation. The bulk of the book (153 pages) consists of the species accounts. For

the North American ornithologist the most interesting features are the accounts of the sixty-four species of Nearctic origin plus eleven species of probable Nearctic origin, and the tables, maps, and histograms. Most of the Nearctic species are waterbirds, but passerines are also being recorded with increasing frequency. One of the tables shows that the Irish Checklist is increasing by an average of 2–3 species per year. Of considerable interest are the tables and maps showing the numbers of breeding seabirds and colony locations since Ireland contains some of the most important seabird colonies in the North Atlantic.

The text is written for the well informed birdwatcher, requiring detailed knowledge of Irish birds, their numbers, probable sources of their origin, population trends and banding recoveries. The book adequately fulfils all these aims. The writing style is fluid and free of technical jargon. I can only find a few small typographical errors.

I recommend this book as a useful addition to the bookshelves of private and institutional libraries requiring a book on Irish birdlife.—STEWART HOLOHAN.

BIRD SONGS IN CUBA [CANTOS DE AVES EN CUBA]. By George B. Reynard, sound recordist, and Orlando H. Garrido, resident ornithologist. Cornell Laboratory of Ornithology, Ithaca, New York. 1989. Two 12 inch, 33⅓ RPM phonograph records. $9.95.—Considering the state of diplomatic relations (or lack thereof) between the United States and Cuba, this product of collaboration between American and Cuban scientists may come as a surprise to some. It is certainly an exemplary cooperative venture that shows how science can transcend politics and perhaps contribute to the foundation of understanding that will one day bridge the political gap.

These records, produced with the cooperation of the Museo Nacional de Historia Natural, Habana, Cuba, include cuts of the vocalizations of 122 species of Cuban birds. Most were recorded by Reynard, but a few are the work of other recordists. An emphasis (longer cuts, recordings of more individuals) has been placed on Cuban endemics. Recordings made outside of Cuba are included for a few species (e.g., Ivory-billed Woodpecker [*Campephilus principalis*], Short-eared Owl [*Asio flammeus*], Hook-billed Kite [*Chondrohierax uncinatus*]). The Ivory-billed Woodpecker sequence includes some of the recordings made by Arthur Allen and Peter Paul Kellogg in Louisiana in 1935, and, much to my surprise, a very brief "double-rap" sequence which Reynard says he recorded in the Big Thicket of Texas in 1969. To my knowledge this is the first published mention of that recording! The double-rap sequence is of very poor quality, and I sent a taped copy to James Tanner for his comments. Tanner could not identify the sound as that of an Ivory-bill. Reynard indicates that he intends to publish details of the Texas recording at a later date. Details relative to these recordings and the original tapes are on file at the Library of Natural Sounds, Cornell Laboratory of Ornithology.

With very few exceptions, the recordings on this record are of superb quality—the work of a real professional. The most difficult cut is that of the Yellow-breasted Crake (*Porzana flaviventer*) which has a rooster crowing more distinctly than the crake's vocalizations. I have been in the field with Orlando Garrido and am certain that the completeness of these records and the facility with which Reynard obtained recordings was due in large measure to Garrido's expertise and enthusiasm. The value of these records is also enhanced by the clarion announcement of species' names in Spanish and English by Alfonso Silva Lee.—JEROME A. JACKSON.

BIRDS OF THE SEWARD PENINSULA, ALASKA: THEIR BIOGEOGRAPHY, SEASONALITY, AND NATURAL HISTORY. By Brina Kessel. University of Alaska Press, Fairbanks. 1989. Cloth, xii + 330 pp., 21 text figs., 11 bird drawings, 17 tables. ISBN 0-912006-29-3. $34.95.—This book is packed full of information about the birds of a little-known area, much of it wilderness, and is one of the few publications to treat an Alaskan avifauna in detail. It is testimony to the author's credentials that she has been involved with most of the other such books in recent years.

What should characterize a good avifaunal study? First, it should be accurate and thorough. It should include information about distribution, abundance, historical changes, habitat use, and seasonality. The region and its birds should be placed in perspective to a larger geographic picture. "Natural history," including a variety of information about the biology of each species, can be considered frosting on the cake, but tasty frosting indeed if the birds are not well known.

How well has Brina Kessel's book satisfied these criteria? I would say very well indeed. The text is carefully organized, with comparable information presented in the same sequence for each species. Consistency of presentation was enhanced by the high latitude, where most species are summer visitors and breeders, but migrants and vagrants are treated in similar detail. Subheadings under each species would have helped the reader relate to this organization even better.

For each species, the distribution within the region is given in detail, including an excellent summary of habitat preferences. Occurrence on the peninsula is placed in the context of the overall distribution and migration routes of each form. A summary of arrival dates, temporal spread, and magnitude of spring migration is followed by the breeding phenology, the latter in substantial detail where known. Brief summaries of breeding and feeding ecology follow, and the account ends with summaries of fall migration and departure dates.

For many species, documentation of occurrence is extensive. Records are listed into 1988, a commendable effort to keep the work up to date. The author also continued to search the literature as she wrote; the extensive list of references includes 12 citations from 1985, 11 from 1986, and six from 1987.

The book serves as a fine example of the importance of unpublished records to regional bird studies. With only museum and literature records, it would have been considerably less valuable. The number of records listed that had not been published elsewhere is testimony to the author's attempt at completeness, as it is always difficult to track down such information. Would that all observers visiting poorly known areas keep complete records and submit them immediately to the appropriate compilers!

As so much of the information available stems from only the last three decades, few historical changes could be documented, although population trends are mentioned for a few species of waterfowl and Sandhill Cranes (*Grus canadensis*).

Although the season of occurrence of most species is relatively short on the Seward Peninsula, details of phenology are given the important status they deserve in the species accounts. I would have liked to see these details also expressed graphically, by relative abundance or number of records in each week-long period, for example. From the author's own substantial field work, there should have been enough information available to do so.

The book is an excellent source of information about breeding biology of arctic and boreal birds, at least those known to breed on the peninsula. I checked the accounts for the shorebirds—of special interest to me—and found them to be accurate and current.

The introduction is concise but adequate. Although the vegetation seems rather uniform to a casual visitor, the fine distinctions among the surprisingly diverse habitats are made clear in the descriptions. Tables of comparative bird abundance, rarely seen in such works,

furnish valuable information for ecologists interested in Arctic and subarctic animal populations as well as birders intending to visit the area.

The Seward Peninsula seems to reach for the coast of Siberia across the narrow Bering Strait, and its avifauna reflects this proximity. Tables showing the zoogeographic affinities of the birds of the peninsula indicate a small proportion of the breeding species but about half of the casual or accidental visitors as coming from Siberia. I found so little to quibble about in this book that I was surprised to see a few species misclassified, in my estimation, in these tables. These species include *Melanitta perspicillata* (North American, not Panboreal), *Arenaria interpres interpres* (Old World, not Panboreal), *Calidris melanotos* (North American, not Beringian), *Rissa tridactyla* (subspecies *R. t. pollicaris* should be listed under Beringian, not the species under Panboreal), and *Carduelis flammea flammea* (Panboreal, not Old World).

Furthermore, I think the Beringian avifauna should be considered as part of a larger picture, and *Pluvialis dominica fulva, Limosa lapponica baueri, Calidris ruficollis, Larus argentatus vegae, L. schistisagus, Phylloscopus borealis kennicotti,* and *Motacilla flava tschutschensis,* listed as Beringian, should be considered Old World, emphasizing that these species, and most of the subspecies, originated in Siberia. *Larus canus brachyrhynchus* (listed as North American) should also be considered in the same category, the subspecies Beringian but the species presumably of Old World origin. On the other hand, *C. mauri* is North American. These are subjective views rather than substantive criticisms, as other authors have listed some of these forms as Kessel did.

I was not looking for typographical errors and saw few of them, but one that jumped out at me was "arcivolines" for arvicolines on page 228; the spelling was correct elsewhere.

The black-and-white bird illustrations by John C. Pitcher have the same crispness and high quality as those of Roger Tory Peterson at his best; both artists should be pleased by the comparison. A long-time Alaska resident, Pitcher *knows* these birds.

For anyone interested in birds of the far North, I recommend this book as interesting and informative. For students of Alaska bird life, it will be required reading.—Dennis R. Paulson.

The Birds of Illinois. By H. David Bohlen, illus. by William Zimmerman. Indiana University Press, Bloomington and Indianapolis, Indiana. 1989:221 pp., 49 color plates with captions, 2 figs., $49.95.—It has been about a century since Robert Ridgway (1889, 1895) completed his two volumes on the Ornithology of Illinois. Bohlen's book is the next complete text on the birds of Illinois, although there have been at least three state checklists, one by Bohlen himself in 1978. The book follows the pattern of many state bird books, but provides more data than most. The lovely, original paintings by Zimmerman run the gamut from a Common Loon (*Gavia immer*) to passerines, with typical habitats where the birds may be found. All the paintings are pleasing, and some show both sexes (e.g., the Common Goldeneye [*Bucephala clangula*], American Kestrel [*Falco sparverius*]), and a few even show food items (e.g., Double-crested Cormorant [*Phalacrocorax auritus*] with a Bluegill, an Osprey [*Pandion haliaetus*] with a river redhorse). Names of species and their order in the list follow the "AOU Check-list of North American Birds, 6th edition" (1983). Subspecies are generally listed, and sometimes discussed, follow the Fifth (1957) Edition of the Check-list. There are about 500 literature citations in the book and an annotated list of 439 species (35 hypothetical, 4 extinct, 4 extirpated, and 99 vagrants—species out of their normal range).

There is a hard-hitting section on conservation in Illinois, with among other things, special mention and discussion of overpopulation by *Homo sapiens,* direct destruction of habitat, and intensive agriculture, followed by a plea for the preservation of the planet's diversity. The status of birds, and the relative abundance are appropriately very much as they are in the Birds of Indiana by Mumford and Keller (1984). One way in which the Illinois book differs is that the status is indicated immediately after the name at the beginning of each account. Birdwatchers can profit from the accounts just for their tips on identification (see especially those on the ducks, and shorebirds). The gull fauna is unexpectedly large in both Illinois and Indiana, both inland states. Typographical errors are few, and there is a wealth of data in this book. It could be read profitably by anyone interested in birds, especially by anyone interested in the midwest.—Richard R. Graber.

An Annotated List of the Birds of Bolivia. by J. V. Remsen, Jr. and Melvin A. Traylor, Jr. Buteo Books, Vermillion, South Dakota, 1989:79 pp., 1 text fig., 3 tables. $15.00.—Remsen and Traylor's annotated list provides the first comprehensive treatment of Bolivian birds since Bond and Meyer de Schauensee's annotated lists of 1942 and 1943. Much inventory work has occurred in the intervening period; most recently, Remsen and the Louisiana State University's Museum of Natural Science staff and students have made Bolivia the focal point of their highly regarded neotropical program.

The wealth of information that has accumulated since Bond and Meyer de Schauensee's treatise is thoroughly and concisely presented in the form of an Introduction, a 30 page Main List, Taxonomic Footnotes, Hypothetical List, followed by an exhaustive Bibliography (nearly 250 references).

The front cover is adorned with the endemic Red-fronted Macaw (*Ara rubrogenys*), skillfully portrayed by John P. O'Neill in its natural setting. A map depicting the habitats and departments of Bolivia is given on the page facing the Introduction and on the back cover. Learning these geographical features is a prerequisite for comprehending the distribution of Bolivian birds. In the Introduction, a short explanation is presented on why Bolivia ranks among the top countries of the world in avian diversity. Currently nearly 1280 species have been recorded in this landlocked country, with the distinct possibility that another 80+ species (presented in a table) may eventually be found there. A brief summary of the topography and the natural divisions is given, followed by some detail on the distribution and status of the sixteen endemics.

The authors give a succinct history of the country's ornithological investigations since the Bond and Meyer de Schauensee lists and then underscore what areas need to be worked to provide a more complete distributional picture. The format of the Main List is discussed in the final pages of the Introduction. Two additional tables summarize the number of bird species in each "life zone" and the frequency of "life zone" distributional patterns for the avifauna, e.g., 404 species (32%) of the Bolivian avifauna are primarily found in the Amazonian lowlands.

Then comes the "heart" of the list. An innovative approach has been used to summarize the distribution of birds in this largely underappreciated, rich avifauna. A numbered reference, usually pertaining to the first departmental specimen record, is given under each department heading for which a species has been recorded. One is thus given an unambiguous picture of how widespread each species is at the departmental level. The final column gives the principal "life zones" in which each species is encountered. No relative abundance designations are given for species, presumably a reflection on the lack of accurate information on this aspect on a country wide basis.

The Taxonomic Footnotes section not only provides current taxonomic opinions on the more controversial Bolivian taxa at the species level, but it also gives the uninitiated, or those who have not kept pace with the rather dramatic changes that have transpired over the past few years, an overview on the more far-reaching, higher level taxonomic clarifications (see especially footnotes 20, 27, 29, 40). The Hypothetical List is a must for any serious student of avian distribution in South America, as it is here that many erroneous, previously published records are corrected (see especially the final two paragraphs of this section).

Given the number of English and scientific names, I was surprised to find only a couple of typographical errors. It is unfortunate that the same style of type that the publishers used in Parker et al.'s (1982), easily readable "An Annotated Checklist of Peruvian Birds" was not again used. The poor quality type gives each letter and symbol a ragged, blurry appearance. After reading a few pages my eyes became fatigued.

I highly recommend this book to every neotropical enthusiast; the taxonomic footnotes and bibliography alone are worth obtaining the work. Moreover, workers who are contemplating doing an annotated check-list of a relatively large, poorly known region, should give serious consideration to the format used by Remsen and Traylor. Anyone planning to visit Bolivia, even on a casual birdwatching trip, will find it indispensible. Conservation organizations will benefit greatly from the distributional and "life zone" information.—Mark B. Robbins.

The Birds of Sicily. By Carmelo Iapichino and Bruno Massa. British Ornithologists' Union, Publication II, % Zoological Museum, Tring, Hertsfordshire, United Kingdom, 1989: 170 pp., 16 black-and-white plates with captions, 8 numbered text figs., 1 table, a gazetteer, 2 appendices. £16.00 UK and £18.00 overseas (postage included).—This is the latest in a series of regional checklists published by the BOU, and it provides a concise summary of the status of each of the 363 species of birds accepted by the authors on the Sicilian list (30 other species are rejected [Appendix 1]). Summaries include information on seasonal occurrence, abundance, habitat associations, distribution, breeding, and banding recoveries (these are detailed in Appendix 2), plus taxonomic and other comments as appropriate. As with any checklist, this section comprises the core of the work—and it is done well. Other topics covered in the book deal with the island's ornithological history, geography, climate, and habitats (including photographs), plus analyses of the avifauna, a section on conservation, gazetteer, and bibliography.

Sicily lies in the southern Mediterranean Sea, separated from the rest of Italy by the Straits of Messina—which are 3-km wide at their narrowest point. Sicily and its 14 associated islets represent the largest of the Mediterranean islands, with a total land area of 25,780 km^2. Elevations range from sea level to 3350 m at the summit of the famous Mt. Etna. Ecological diversity is correspondingly high, but thousands of years of human occupancy have taken a great toll on the island's natural habitats—which range from salt pans to montane forests of pine (*Pinus*), fir (*Abies*), birch (*Betula*), beech (*Fagus*), chestnut (*Castanea*), and maple (*Acer*). Historically, the most widespread habitats were woodlands and Mediterranean scrub, which are characterized especially by oaks (*Quercus* spp.), heaths (*Arbutus* and *Erica*), and other plants—many of which are sclero- and/or microphyllous. Cultivated plants—several being exotic in origin—are widely distributed on the island and include olives (*Olea europea*), carobs (*Ceratonia siliqua*), citrus, Australian *Eucalyptus* and *Acacia,* and even New World

cacti (*Opuntia*) and century plants (*Agave*). Aquatic habitats include rivers, lakes, and marshes, but these have been largely modified or destroyed by humans—at least 5,000,000 of which live on the island.

The first broad treatise on the Sicilian avifauna was published in 1840, although earlier works dealing with the island's birds date from the thirteenth century. Iapichino and Massa have published on the island's birdlife for a combined total of over 35 years, beginning in 1974 and 1969, respectively. One of Massa's important publications was on the results of a breeding-atlas survey in 1979–1983. This showed 135 species of birds breeding in Sicily, with 31 occurring in 50% or more of the 297 10-km^2 quadrates that encompass the island and its islets. Other interesting revelations about the breeding avifauna include the facts that a thousand or more pairs of British Storm-Petrels (*Hydrobates pelagicus*), Cory's Shearwaters (*Calonectris diomedea*), Manx Shearwaters (*Puffinus puffinus*), and Yellow-legged Gulls (*Larus cachinnans*) breed on or around Sicily. On the other hand, several avian species no longer breed on the island—these consisting mainly of wetland inhabitants, raptors, and gamebirds.

Sicily is also important for wintering and migrant birds, as one would expect from its location. Notable among wintering birds are various waterfowl, gulls, and certain passerines. In terms of migration, species diversity is high; however, numbers are only moderate, in spite of Sicily's position as a land link between Europe and North Africa (Tunisia lies only 145 km to the south-southwest). The fact is that bird migration progresses on a broad front across the Mediterranean (as well as the Sahara); consequently, seemingly favorable areas such as Sicily do not actually produce the concentrations of migrants that one might otherwise expect.

As in several other parts of the Mediterranean Basin, many birds are killed for sport and other purposes in Sicily. For example, Iapichino and Massa present data showing 938 hunter-killed raptors (30 species) being processed by eight taxidermists in the winters of 1981 and 1983! Such birds are not legal game, and in fact nongame birds bear the brunt of the killing on the island. Shooting of migrant birds on both sides of the Straits of Messina leads to the slaughter of thousands of individuals—including at least 1000 Honey Buzzards (*Pernis apivorus*) each year. Coupled with the effects of the loss of habitat and other negative impacts, Iapichino and Massa aptly refer to Sicily as a "blackspot" in terms of bird protection in the Mediterranean Basin.

Although Sicily has a decidedly bleak side as regards its birdlife, the island and associated islets support a rich and interesting avifauna. For anyone wanting detailed information on the subject, this book is a must—and I recommend it as well for anyone whose interests include any part of the Mediterranean Basin. In my view, the authors have done an excellent job of elucidating the Sicilian avifauna and its challenging environment—warts and all. The major thing that I think could have improved the book would have been the addition of Sicilian names for each species, which would have aided birders visiting the island.—John P. Hubbard.

Key Forests for Threatened Birds in Africa. By N. J. Collar and S. N. Stuart, in collaboration with the I.U.C.N. Species Survival Commission. I.C.B.P. Monograph No. 3. I.C.B.P., Cambridge, England, 1988. 102 pp., 7 maps, 1 table. £7.00.—This useful study is essentially a spinoff from the authors' landmark compendium (1985) *Threatened birds of Africa and related islands: the ICBP/IUCN Red Data Book, part 1 (3rd edition).* In the latter the focus is on the status of individual bird species; here the emphasis is on the forests they live in. Seventy-five of the most threatened and biologically important forests of Africa and the Malagasy Region have been selected according to criteria set forth in the introduction. (The Malagasy Region is incorrectly assumed to be part of Africa; however, for reasons of

geographic proximity, if not of biogeography, it is probably best included here.) Each forest has been given a priority score based on Red Data Book categories, and a table in the introduction lists them by rank. Two maps show their locations, supplemented by five larger scale maps covering areas where clusters of them occur. In the main body of the text are accounts of each forest, averaging about a page. They begin with a brief summary of geology, vegetation and climate, including a list of dominant tree species. Threatened birds are discussed and given a symbol indicating their status. Other threatened forms are also listed, principally mammals but also other vertebrates, invertebrates and plants, underlining the fact that the work is not concerned only with birds. Lastly the condition of each forest is assessed, current and future threats summarized, existing and proposed legislation and conservation plans described, and recommendations made.

This little book will serve as a handy manual for all those concerned about the future of African forests (and who among us is not?), and as ammunition in the fight for their preservation. Governments can no longer pretend they don't have enough information on which to base environmental programs. The authors are to be congratulated on this production, and I.C.B.P. is to be lauded for their continuing series of publications on endangered birds and their habitats.—STUART KEITH.

BIRDS ASLEEP. By Alexander F. Skutch, illus. by N. John Schmitt. University of Texas Press, Austin, Texas, 1989. 219 pp., 29 black-and-white drawings $24.95.—During winter, White-breasted Nuthatches (*Sitta carolinensis*) take shelter singly at night in holes in trees, often ones initially carved out by woodpeckers. At any time of year, Rufous-fronted Thornbirds (*Phacellodomus rufifrons*) sleep together as family groups in the bulky and elaborate nests they use for breeding. Verdins (*Auriparus flaviceps*) build breeding nests but also construct nests to be used exclusively for sleeping, large ones for cold weather and flimsier ones for summer use. Most birds spend at least half their lives inactive, sleeping, or resting, yet facts such as these are unfamiliar because ornithologists have studied almost exclusively the active portions of their subjects' existences. In this volume the distinguished tropical naturalist, Alexander Skutch, seeks to redress this imbalance by reviewing all that is known about where, when, and how birds sleep. As Skutch argues, knowing how birds "pass the more obscure half of their lives is necessary to round out our picture of their habits."

Skutch has scoured the published literature for facts on birds at rest, and in addition has himself gathered a great many observations over his decades of studying neotropical species. This has entailed examining likely resting places at night with a flashlight, and patiently staking out such sites late in the evening or very early in the morning for glimpses of arriving and departing individuals. Skutch begins his book by reviewing what is known about the sleeping habits of oceanic and freshwater birds, and about those terrestrial species that rest in simple, unmodified sites. The bulk of the book is devoted to birds that sleep in "dormitories," defined by Skutch as "any sheltered place, other than a perch amid vegetation, the ground, or water, used by a fledged bird or birds for sleeping when neither incubating eggs or brooding young." This loose definition takes in nests, both those built for breeding and subsidiarily used for sleeping and those built exclusively for resting, holes in trees and in the ground, nooks and crannies in manmade structures, and a variety of other sites. Skutch concentrates mainly on structures built or modified by birds themselves, and perhaps it would have been better to confine the term dormitory to these.

Skutch describes eight categories of sleeping behavior that he believes represent stages in the evolution of the dormitory habit. In the early stages, the breeding nest is used for resting, first by the female alone, then by both parents, and then by the young after fledging, either alone or with the parents. In the later stages, a nest or nesthole is constructed or stolen solely

for sleeping, first for use by individuals, then by pairs, parents with fledglings, parents with self-supporting young, and in the final stage by larger groups. Skutch is almost certainly correct in maintaining that dormitories originated from breeding nests, but it seems unlikely that the sequence he lays out was always followed in evolution; for example, there seems no necessity for use of a breeding nest for sleeping by parents always to precede use by fledglings, or for use of a breeding nest by fledglings always to precede use of a nonbreeding nest by pairs. Nevertheless, the system of categories is useful in organizing the facts on dormitory use.

Judged on scientific content, the book suffers from Skutch's reliance on outmoded aspects of evolutionary theory, particularly group selectionism of a primitive type. Further, some readers may be put off by Skutch's readiness to ascribe to birds a variety of human thoughts and emotions. However, these sins of interpretation are minor faults compared to the service Skutch has done in gleaning and compiling the array of observations presented here. Judged as literature, the book is beautifully written, and enlivened by entertaining facts and anecdotes. My only complaint here is that the repetition of examples of particular behaviors can become tedious, as when one reaches the twentieth example of dormitories used as family dwellings. Still, taken individually these examples are fascinating, and they constitute the true attraction of the book. Certain vignettes are wonderful, as for example Skutch's description of his visit to a cavern where Oilbirds (*Steatornis caripensis*) rest by day. After a long walk through tropical forest, Skutch enters the great cavern, whose floor is covered by a strange carpet of seeds, regurgitated by the Oilbirds and now eerily germinating in the darkness. The birds themselves perch on shelves of rock high overhead, so far above that a flashlight reveals "scarcely more than the ruby eyes of dusky birds dimly seen: innumerable pairs of gleaming red eyes, crowded companies of eyes, long ranks of eyes, shining from all the high, inaccessible ledges." Quite apart from the scientific value of the volume, scenes such as this are alone sufficient to make the book rewarding.—William A. Searcy.

Introducing Birds to Young Naturalists. By Ilo Hiller. Texas A&M University Press, College Station. 1989:69 pp., 36 color plates, 3 black-and-white plates, 9 figs., 1 table. $21.50 cloth, $12.95 paper.—This book is a well-written introduction to bird study emphasizing species of Texas and the southwest. Most of the chapters first appeared in "Texas Parks and Wildlife," and the fine color photographs and self-contained nature of these chapters reflect the original magazine format. Five chapters introduce the reader to bird feathers, eggs, songs, bird houses, and feeders. These are followed by chapters on bluebirds, cardinals and Pyrrhuloxias, woodpeckers, killdeer, owls, roadrunners, cuckoos and anis, doves and pigeons, mockingbirds, jays, and hummingbirds. The writing is at a relatively advanced reading level, so adults will have to read and interpret the content for young children. There are aids for pronunciation and definitions and translations of scientific names. There is no advice on optical equipment or birdwatching technique, although there are chapters on bird houses and feeders. Everyone will enjoy the striking color photographs.—Albert R. Buckelew Jr.

CORRECTION

The authors of the paper " Brood adoption and apparent infanticide in a north-temperate House Wren population" in *The Wilson Bulletin* 102:333–336, 1990, are L. Henry Kermott and L. Scott Johnson.

Wilson Bull., 102(4), 1990, pp. 743–755

PROCEEDINGS OF THE SEVENTY-FIRST ANNUAL MEETING

JOHN L. ZIMMERMAN, SECRETARY

The Seventy-first Annual Meeting of the Wilson Ornithological Society was held Thursday, 31 May to Sunday, 3 June 1990 at Wheaton College, Norton, Massachusetts in joint session with the Association of Field Ornithologists. The local committee chaired by Dr. John Kricher was composed of William E. Davis, Jr., Janet L. Heywood, Betty Petersen, Wayne R. Petersen, Martha Steele, and Martha Vaughan. The meeting was sponsored by the Biology Department of Wheaton College, *Bird Observer,* Manomet Bird Observatory, Massachusetts Audubon Society, and the Nuttall Ornithological Club.

The Council met from 13:10 to 21:40 on Thursday, while registration from the 190 guests and members began in the Science Center. On Thursday evening a reception in the Balfour Hood Center was hosted by the Nuttall Ornithological Club. The opening session on Friday convened in the Auditorium of the Science Center where the Society was welcomed by Dr. Hanna Goldberg, Provost and Academic Vice-president of Wheaton College. President Jon C. Barlow responded for the Wilson Ornithological Society, and President Peter F. Cannell responded for the Association of Field Ornithologists.

The scientific papers sessions, which included contributed papers, a workshop on field techniques and data management for banders chaired by Christopher Rimmer, a workshop on conservation of coastal wetlands in the western hemisphere chaired by Keith Bildstein, and symposia on the amateur in ornithology and American avian zoogeography were held on Friday and Saturday in the Science Center. Poster papers were presented in the Balfour Hood Center, highlighted by a reception Friday evening hosted by Wheaton College and the Manomet Bird Observatory. Field trips on Sunday included a pelagic whale watch and an excursion to Plum Island.

The annual banquet was held in the Emerson Dining Hall on the campus Saturday evening, after which the following awards were presented:

EDWARDS PRIZE (for the best major article in volume 101 of The Wilson Bulletin)

David E. Blockstein, "Crop milk and clutch size in Mourning Doves," Wilson Bulletin 101:11–25.

LOUIS AGASSIZ FUERTES AWARD

Erika Deinert, "The evolution of cooperative courtship displays in male Rio Grande Turkeys."

MARGARET MORSE NICE AWARD

Carolyn A. Drake, "Creating a scientifically accurate and appropriate bibliography for the study of birds so that it can be utilized in the educational curriculum of youth from kindergarten through the eighth grade."

PAUL A. STEWART AWARDS

Stephen P. Flemming, "Do Red-winged Blackbird colonies and roosts function as information centers?"

Gustavo J. Inglesias, "Birds of the understory subtropical rainforest of the Iguazu National Parks, Argentina."

Jeffery S. Marks, "Nonbreeding ecology of Bristle-thighed Curlews on Laysan Island, Hawaiian Islands."

Satu K. Pernanen, "The role of eco-behavioral data in assessing species limits in *Spizella*."

David R. C. Prescott, "Differential migration in the Evening Grosbeak: A test of an hypothesis."

Jeffery V. Wells, "Dispersal, site fidelity and mortality rates in an isolated population of grassland birds."

Hsiao-Wei Yuan, "Demography, dispersal, and population structure of Common Tern (*Sterna hirundo*) at Oenida Lake, New York."

ALEXANDER WILSON PRIZE (for best student paper)

Lynn A. Mahaffy, Dept. Natural Resources, Cornell Univ., Ithaca, NY, "Water off a duck's back: Is feather structure a key to water-repellency?"

Selection committees for these awards: Edwards Prize—Charles Blem, Mark Colwell, Chris Stinson, and Anne Wenner; Fuertes, Nice, and Stewart Awards—Richard Banks and Richard Stiehl; Wilson Prize—Richard Banks, Herb Hendrickson, and Ernest Willoughby.

The evening was delightfully completed with a presentation by Dr. Frank B. Gill, Academy of Natural Sciences, Philadelphia, PA on, "The Quest for Pere David's Tit."

FIRST BUSINESS MEETING

The first business meeting was called to order by President Barlow at 11:33, Friday, 1 June in the Science Center auditorium. Secretary Zimmerman summarized the highlights of Thursday's Council meeting. Next year the Society will meet with the Cooper Ornithological Society at the University of Oklahoma, Norman, OK, from 15–19 May 1991 with Professor Gary Schnell as the local chairperson. In the following year the meeting will be in the Orlando-Kissimmee area and be sponsored by the Lake Region Audubon Society, Archbold Biological Station, and the Florida Ornithological Society (dates to be announced). The treasurer has reported the Society in excellent shape with income exceeding expenses by $14,068. The proposed budget for next year totals $95,000. The present membership is 2249 and reflects a 1 percent decrease from the previous year. John Smallwood, chair of the membership committee, is preparing a new membership brochure and encourages all members to seek copies for distribution to potential members. OSNA administrative activities are to be shifted to Allen Press, Lawrence, Kansas, but Sandra L. L. Gaunt will continue as Director, at least for an additional year. Charles Blem has been reelected as editor. New business of note is the plan to develop travel awards for students and amateurs giving papers at future meetings. The Sutton Prize will be offered again, appropriately at next year's meeting in Norman, Oklahoma. J. Wm. Hardy has accepted chairpersonship of this bird art competition. Lastly, Zimmerman asked the membership to stand in honor of members who had died since the last annual meeting—Richard O. Albert (Alice, TX), Laurence L. Alexander (Gainesville, FL), Mrs. Allan G. Davenport (Providence, RI), Annette Duchein (Ocean Springs, MS), Mrs. John Fiske (Petersham, MA), Michael Harwood (Washington, CT), Mrs. John W. Lueshen (Wisner, NE), John M. McCormick (Ashland, OR), Robert M. Mengel (Lawrence, KS), Kenneth D. Morrison (Babson Park, FL), Frank W, Preston (Butler, PA), Hugh L. Quarles (University, MS), Norman F. Sloan (Houghton, MI), Frank B. Smithe (Douglaston, NY), Doris H. Speirs (Pickering, ON), Jane E. Stern (Pine Bluff, AR), Mrs. W. C. Stone, Sr. (Clinton, SC), Elmer W. Strehlow (Green Bay, WI), Mrs. Anne Hinshaw Wing (Colorado Springs, CO), and Wendell L. Whittemore (Memphis, TN).

J. D. Rising presented the report of the nominating committee: Jon C. Barlow, president; Richard C. Banks, first vice-president; Richard N. Conner, second vice-president; Robert D. Burns, treasure; John L. Zimmerman, secretary; Frank Gill and Bette Jackson for three-year terms as councilors.

Robert D. Burns gave the treasurer's report.

REPORT OF THE TREASURER
1 JANUARY 1989 TO 31 DECEMBER 1989

GENERAL FUNDS

RECEIPTS		
Regular and Sustaining Memberships for 1989	$ 15,096.00	
For 1990	15,969.00	
Student Memberships for 1989	1,313.00	
For 1990	1,166.00	
Family Memberships for 1989	175.00	
For 1990	500.00	
TOTAL DUES		$ 34,219.00
Subscriptions to *The Wilson Bulletin*		
For 1989	$ 20,491.00	
For 1990	7,138.50	
TOTAL SUBSCRIPTIONS		$ 27,629.50
Back Issues of *The Wilson Bulletin*		$ 309.50
Interest and Dividends		$ 21,044.79
Royalties		$ 3,571.45
Contributions from Authors		$ 11,067.40
Contributions to The Van Tyne Library		$ 114.00
Contributions to the Student Membership Endowment		$ 826.49
Contributions to General Endowment (Life Members and Patrons)		$ 1,000.00
Contributions to the Edwards Prize		$ 350.00
Contributions to the Wilson Prize		$ 54.00
Sale of Computer		$ 200.00
TOTAL RECEIPTS		$100,386.13
DISBURSEMENTS: 1989		
The Wilson Bulletin		
December 1988	$ 18,403.05	
March 1989	14,159.91	
June 1989	18,547.87	
September 1989	14,790.49	
Total Printing and Mailing	65,901.32	
Editor's Expenses	3,714.50	
Color Plates	0.00	
TOTAL PRODUCTION COSTS		$ 69,615.82
OSNA Expenses*		$ 9,330.00
Student Awards		$ 2,650.00
Treasurer's Expenses		$ 189.92
Treasurer's Bond		$ 100.00
Mailings, Student Membership Award Notices		$ 39.65

AAZN Dues		$ 100.00
ICBP Dues		$ 0.00
Subscriptions and OSNA Refunds		$ 60.00
Printing and Mailing of Back Issues		$ 1,048.55
Incorporation Fee		$ 5.00
Deposit to Endowment		$ 1,880.49
Meeting Expenses		$ 593.01
Wilson Stationery		$ 89.90
President's Expense (Postage)		$ 33.74
Van Tyne Library		$ 582.00
TOTAL DISBURSEMENTS		$ 86,318.08
Note: *Newsletter about $3,000.00		
BALANCE—Income Less Disbursements		$ 14,068.05

CASH ACCOUNTS

Peoples Bank, Gambier, OH 43022 31 December 1989		
Checking Account	$ 13,979.98	
Dreyfus Liquid Assets	59,976.44	
TOTAL CASH ON HAND		$ 73,956.42

DESIGNATED ACCOUNTS

Louis Agassiz Fuertes and Margaret M. Nice Awards

Endowment Principal		$ 10,000.00
1989 Earnings	$ 700.00	
1988 Balance	$ 200.00	
Award Funds Available	$ 900.00	
Funds Disbursed for Awards	$ 400.00	
1989 Cash Balance	$ 500.00	

Alexander Wilson Prize

Endowment Principal		$ 2,396.41
1989 Earnings	$ 167.75	
1988 Balance	$ (168.65)	
Funds Available	$ (0.90)	
Funds Disbursed for Awards	$ 100.00	
1989 Cash Balance	$ (99.10)	

Paul A. Stewart Awards

Endowment Principal		$ 22,850.37
1989 Earnings	$ 1,599.53	
Funds Disbursed for Awards	$ 1,800.00	
1989 Balance	$ (200.47)	

George Sutton Color Plate Fund

Endowment Principal		$ 50,000.00
Funds Available 1989	$ 945.86	
1989 Earnings	$ 3,500.00	
Funds Disbursed for Color Plates	$ 0.00	
1989 Cash Balance	$ 4,445.86	

Ernest P. Edwards Prize

Endowment Principal		$ 2,695.90
Funds Available	$ 350.00	
Funds Disbursed for Awards	$ 350.00	
1989 Cash Balance	$ 00.00	

General Endowment Funds

Endowment Principal 1988	$151,786.00
1989 Balance of General Endowment Principal	$158,222.32

TOTAL ENDOWMENT FUNDS

1988	Amount Invested (Carrying Value)		$247,720.00
	Market Value		$320,236.00
1989	Deposited to Endowment	$1,880.49	
	Sale and Purchase of Securities	$ 984.51	
	Endowment Principal as of 12-31-89		$250,585.00
	Market Value as of 12-31-89		$386,992.00

Annual Meeting Reserve Funds

1989 Cash Balance		$ 4,338.77
1989 Meeting Expenses	$ 593.01	
1989 Balance of Centennial Meeting Funds		$ 3,745.76

Robert D. Burns, TREASURER

EDITOR'S REPORT—1989

In 1989, 171 manuscripts (62 major papers, 109 short communications) were submitted to *The Wilson Bulletin* office. This is only one paper less than submitted in 1988. Of these, 51% have been accepted, 46% have been rejected, and 3% remain under review. Our acceptance rate remains nearly 60% for major papers and about 45% for short communications. These figures are not exact. Frequently, manuscripts submitted as major papers are converted to short communications. There presently is no backlog of frontispiece articles and any manuscript which is accepted and includes a relevant color plate is given rapid attention. On the average, papers received in 1989 were returned to the author within about 65 days of receipt. Those papers which require more time in the editorial process are always delayed by tardiness of referees.

I am grateful to my Editorial Board, Kathy G. Beal, R. N. Conner, C. H. Stinson, and J. R. Walters. Besides acting as "super-referees", they often give me advice about dealing with specific problems. Review editor George A. Hall continues to provide timely and interesting book reviews. I remain indebted to Assistant Editors Leann Blem, Albert E. Conway, and Anne Wenner, whose attention to detail not only keeps our error rate down, but also saves the society money. Karen Blem and Leann Blem deserve special acknowledgment for running the editorial office. I am especially grateful to Kathy G. Beal who has prepared the index for WB for several years. This little-noticed task makes the journal more useful for all of us.

We remain committed to quality and to serving our readers. We try to treat all authors

with consideration and with the goal of helping them to find a home for their manuscripts. Any suggestions toward improving that process will be considered seriously.

C. R. Blem, *Editor*

The meeting was temporarily adjourned until the second session.

SECOND BUSINESS MEETING

President Barlow opened the second business meeting at 13:18, Saturday, 2 June in the Science Center. The report of the Auditing Committee was received.

We, the undersigned, met on 1 June 1990 to scrutinize the financial records presented to us by the treasurer for the period 1 January 1989 to 31 December 1989. Upon reviewing these records, consisting of bank statements, cancelled checks, OSNA payments, etc., we are satisfied that they accurately reflect the financial operations of the Society and that the treasurer pays the bills and deposits the receipts in a timely manner. We believe that the balances shown for the General, Designated, and Endowment Funds are accurately stated. The committee members commend Dr. Robert Burns for his continuing diligent performance in fulfilling the duties of treasurer for 1989 and for maintaining sound fiscal controls of the Society's assets.

Hubert P. Zernickow, *Chairperson*
Harold Ratcliff
Robert A. Whiting

It was moved by Chan Robbins and seconded by Mary Clench to accept this report, and the motion passed.

President Barlow recalled the report of the nominating committee to the floor of the assembly. Additional nominations from the floor were requested, but none were offered. George Hall moved and Mary Clench seconded that the nominations be closed and that a unanimous ballot be cast. The motion passed, and a unanimous ballot was duly recorded by Doris Watt, who was acting secretary.

George Hall presented the report of the resolutions committee.

REPORT OF THE RESOLUTIONS COMMITTEE

WHEREAS, coastal wetlands comprise less than 3% of the land surface of the Western Hemisphere, and

WHEREAS, coastal wetlands include some of the most productive and ecologically valuable natural habitats, and

WHEREAS, approximately half of the hemisphere's human population lives near and depends upon these wetlands, and

WHEREAS, these open ecological systems can be used by human populations in a sustainable manner, but

WHEREAS, such wetlands continue to be altered detrimentally, both directly and indirectly, by the actions of human populations throughout the hemisphere at an alarming rate,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society: (1) recommends that appropriate local, state, and national governmental and nongovernmental organizations in the Western Hemisphere enhance and ensure the protection of these important ecological resources by supporting essential research, by the passage of new protective and regulatory legislation as warranted, and by the enforcement of existing laws concerning wetland use, and (2) suggests that programs such as Florida's "Save Our Rivers" and "Surface Water

Improvement and Management" be implemented and used as models elsewhere, and (3) that nations that have not already done so become contracting parties to the Convention on Wetlands of International Importance Especially as Waterfowl Habitat (the so-called RAMSAR Convention), and (4) that all nations adhere to both the spirit and letter of this international treaty and that they actively promote the wise and sustainable use of coastal wetlands within and beyond their jurisdiction.

It was moved by Robert Whiting and seconded by Jeff Spendelow to accept this resolution, and the motion passed.

WHEREAS, Maurice Graham Brooks has been a member of the Wilson Ornithological Society since 1927, and

WHEREAS, he has served the Society as a member of the Council, as Secretary, and as President from 1950 to 1952, and

WHEREAS, he has been a mentor and inspiration to several generations of students in the southern Appalachians, and

WHEREAS, on 16 June 1990 Maurice Brooks will celebrate his ninetieth birthday,

THEREFORE BE IT RESOLVED that we, the members of the Wilson Ornithological Society, assembled at the 71st annual meeting at Wheaton College, Norton, Massachusetts send our warmest birthday greetings and our heartfelt thanks to Maurice Graham Brooks on this very special occasion.

It was moved by Hubert Zernickow and seconded by Chan Robbins to accept this resolution, and the motion passed.

WHEREAS, the Wilson Ornithological Society, together with the Association of Field Ornithologists, have held their joint meeting in the pleasant surroundings at Wheaton College in Norton, Massachusetts, and

WHEREAS, the Biology Department of Wheaton College, and the co-sponsors—*Bird Observer,* the Manomet Bird Observatory, the Massachusetts Audubon Society, and the Nuttall Ornithological Club—have been responsible for the pleasant atmosphere of the meeting, and

WHEREAS, the Local Committee on Arrangements, ably chaired by John C. Kricher, has worked diligently to assure the success of this joint meeting, and

WHEREAS, the Committee on Scientific Program, co-chaired by Richard N. Conner and Edward H. Burtt, Jr., has provided an innovative and interesting program of symposia, workshops, and scientific papers,

THEREFORE BE IT RESOLVED, that the Wilson Ornithological Society commends the sponsoring groups and salutes the Local Committee on Arrangements for a job well done.

Herb Henrickson moved and Richard Stiehl seconded the motion to accept this resolution, it passed with hearty applause.

It was moved by Richard Conner and seconded by Chan Robbins that the meeting be adjourned, and it was.

The reports of the standing committees are as follows.

REPORT OF JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE—1989

During the past calendar year, the activities of the Library have continued to prosper; some moderate drops in the figures both for member-usage and member-donations hopefully must reflect merely normal fluctuations. Some ongoing physical improvements in the UMMZ Bird Division offices and laboratory facilities have affected the WOS library, through some short-term inconveniences but long-term advantages in overall efficiency and comfort. The undersigned chairman, now retired and operating largely from home, has less day-to-day contact with library activity than before. However, Janet Hinshaw continues to be the real

guiding hand in keeping our affairs in order; she deserves all the help and appreciation we can possibly give her with each passing year.

Twenty-four of our generous members donated a total of 517 items to the Library collections: 41 books, 184 serial issues, 127 monographs and reports, and 165 reprints. Donors were R. Bayer, A. J. Berger, R. Breitwisch, M. Clench, M. W. Collopy, R. N. Conner, J. Grabowski, G. A. Hall (WOS review copies), K. Haller, R. Hoffman, S. Holohan, D. James, G. R. Lingle, F. Lohrer, H. Mayfield, T. Miley, R. B. Payne, F. A. Pitelka, W. Post, S. W. Richards, W. Thiede, C. Violani, T. Will, and E. Wolfe. Special thanks are due also for a bequest from the Margaret M. Mitchell estate of 514 volumes, including books, short runs of bird journals, and field notebooks.

We urge even more members to contribute library materials. Items that do not go directly onto our shelves can be equally valuable as duplicates, and for sale to augment the New Book Fund. This year, sales of 26 books and journals netted $345.50. A total of 23 purchases from the fund of 17 books and reports and 6 records and tapes amounted to $603.15.

Through other processes, the Library received a total of 221 titles (serials, monographs, and reprints) from 166 institutions, organizations, and members: 163 titles from 125 exchanges, 41 from 30 gifts, and 17 on 11 regular subscriptions.

Perhaps most importantly—for this constitutes our most direct continuing service to the membership—the WOS library loaned 194 items in a total of 149 separate transactions: 28 members and libraries borrowed 24 books, 153 photocopies, 12 translations, 1 microfilm, 1 reprint, and 3 journal issues. We hope that an increasing number of members will find it convenient to borrow publications for which they find a need from our large collections.

We thank everyone who has in any way contributed to this, another very successful year.

William A. Lunk, *Chair*

REPORT OF THE CONSERVATION COMMITTEE

The committee has organized a round-table discussion for the 71st annual meeting entitled, "Conservation of coastal wetlands in the Western Hemisphere." A manuscript by this title is being prepared for publication in The Wilson Bulletin and will constitute the formal report of the committee.

Keith L. Bildstein, *Chair*

REPORT OF THE MEMBERSHIP COMMITTEE

The information brochure sent in response to inquiries about membership is being revised. Members are asked to send suggestions to the chair, and upon its publication, to request copies for distribution.

John A. Smallwood, *Chair*

The Committee on Scientific Program was co-chaired by Richard Conner for the Wilson Society and Edward H. Burtt, Jr. for the Association of Field Ornithologists. The following members assisted as session moderators: Keith L. Bildstein, Margaret C. Brittingham, Mary H. Clench, Jerome A. Jackson, James D. Rising, Charles R. Smith, Elliot J. Tramer, and Richard H. Yahner.

PAPERS SESSIONS

Mary H. Clench, Dept. Internal Medicine, Univ. Texas Medical Branch, Galveston, TX 77550, "From the pilgrims to the present: the contributions of amateur ornithologists."

Harold F. Mayfield, 1162 Nanette Dr., Toledo, OH 43614, "The amateur: finding a niche in ornithology."

Robert P. Yunick, 1527 Myron St., Schenectady, NY 12309, "Banders as an ornithological resource."

John Tautin, Bird Banding Laboratory, U.S. Fish & Wildl. Service, Laurel, MD 20708, "The amateur bird bander—the Bird Banding Lab perspective."

Francois Vuilleumier, Dept. Ornithology, Amer. Museum Natural History, Central Park West at 79th St., New York, NY 10024-5192, "Origins and development of American avian zoogeography."

Chandler S. Robbins, U.S. Fish & Wildl. Service, Patuxent Wildl. Res. Center, Laurel, MD 20708. "Use of BBS, BBC, and WBPS to track zoogeographic change."

Russell Greenberg, National Zoological Park, Washington, DC 20008, "The destination of neotropical migratory birds."

Elliot J. Tramer, Dept. Biol., The Univ. Toledo, Toledo, OH 43606, "Global warming, vegetation changes, and the future of avian zoogeography."

Margaret C. Brittingham, Pennsylvania State Univ., University Park, PA 16802, "Dynamics of a Blue Jay population: a long-term banding study by Peggy Hickey."

Gregory S. Butcher and James D. Lowe, Laboratory of Ornithology, Cornell Univ., Ithaca, NY 14850, "Dynamic American zoogeography using data collected by amateurs: raptors on Christmas bird counts."

Alison M. Mostrom, Dept. Biology, Univ. Pennsylvania, Philadelphia, PA 19104-6018, "Who initiates group movement in Carolina Chickadee (*Parus carolinensis*) flocks? A test of four hypotheses."

Erica H. Dunn, Laboratory of Ornithology, Cornell Univ., Ithaca, NY 14850, "The relationship between bird numbers at feeders and 'in the wild'."

Philip C. Stouffer, Donald F. Caccamise, and Douglas W. White, Dept. Entomology and Economic Zoology, Rutgers Univ., New Brunswick, NJ 08903, "Roosting and diurnal movements of radio-tagged crows."

Charles R. Smith, Laboratory of Ornithology and Dept. Natural Resources, Cornell Univ., Ithaca, NY 14850, "Volunteer contributions to bird conservation: an example from New York state."

Ralph W. Dexter, Dept. Biological Sciences, Kent State Univ., Kent, OH 44242, "Comparative mating history of female Chimney Swifts (*Chaetura pelagica*) nesting for nine years in a breeding colony."

Eric Strauss and Benjamin Dane, Tufts Univ., Medford, MA 02155, "Reduced fledging success and decreased foraging efficiency of Piping Plover chicks in disturbed habitat."

Peter D. Vickery, Malcolm L. Hunter, Jr., and Jeffrey V. Wells, Wildlife Dept., Univ. Maine, Orono, ME 04469, "A new comprehensive measure of reproductive success: its application to the relationship of habitat quality in three Emberizine sparrows."

Peter D. Vickery, Malcolm L. Hunter, Jr., and Jeffrey V. Wells, Wildlife Dept., Univ. Maine, Orono, ME 04469, "Is increased territorial density associated with higher levels of breeding success?"

Carol A. Corbat, School of Forest Resources, Univ. Georgia, Athens, GA 30602, "Nesting success, nest site fidelity, and nesting habitat of Wilson's Plover in Georgia."

Thomas C. Gumbart, Utah State Univ., Logan, UT 84322–55305, "Drought effects on reproductive success in Yellow-eyed Juncos."

June A. Chamberlain-Auger, 121 Cap'n Lijah's Road, Centerville, MA 02632, "Reproductive success of American Crows living in two different habitat types."

Douglas W. White, E. Dale Kennedy, and Philip C. Stoufer, Rutgers Univ., Piscataway, NJ 08855, "Feather regrowth in female European Starlings rearing different brood sizes."

Richard H. Yahner and Thomas E. Morrell, Pennsylvania State Univ., University Park, PA 16802, "Depredation of artificial avian nests in irrigated forests."

Richard A. Lent, Seatuck Res. Program, Islip, NY and Dept. Ecol. and Evol., SUNY Stony Brook, NY 11790, "A multifactorial analysis of nest predation in the Gray Catbird, with comparison to artificial nests."

R. R. Roth and R. K. Johnson, Dept. Entomology and Appl. Ecology, Univ. Delaware, Newark, DE 19717-1303, "Cowbird parasitism: a factor in the decline of the Wood Thrush?"

Gayle A. Unruh, Burns & McDonnell, Kansas City, MO 64141-6173, and Edwin C. Franks, Western Illinois Univ., Macomb, IL, "A bird on every fencepost."

Jeffrey A. Spendelow, U.S. Fish & Wildl. Service, Patuxent Res. Center, Laurel, MD 20708, "An assessment of various nesting habitat enhancement projects for Roseate Terns at Falkner Island, Connecticut."

E. Dale Kennedy and Douglas W. White, Rutgers Univ., Piscataway, NJ 08855, "Repeatability of clutch size in House Wrens."

Laurie H. MacIvor and Curtice R. Griffin, Dept. Forestry and Wildl. Mgt., Univ. Massachusetts, Amherst, MA 01002, and Scott M. Melvin, Dept. Inland Fisheries and Wildl., Bangor, ME 04401, "Mate retention and site fidelity of Piping Plovers in Massachusetts."

Carola A. Haas, Dept. Natural Resources, Cornell Univ., Ithaca, NY 14853, "The effect of experience on site fidelity."

Jed S. Merrow, Univ. Rhode Island, Kingston, RI 02881, "The influence of area and habitat on red maple swamp bird communities."

Donald J. Smith and Charles R. Smith, Laboratory of Ornithology and Dept. Natural Resources, Cornell Univ., Ithaca, NY 14850, "Use of active pastures by Henslow's and Grasshopper Sparrows in upstate New York."

Leah Schimmel, Biology Dept., Boston Univ., Boston, MA 02215, "An interspecific comparison of individual and species recognition in the passerines *Turdus migratorius* and *Cyanocitta cristata*."

Kenneth E. Petit, 348 Church St., Doylestown, OH 44230, "Roost site selection by the Galapagos Dove (*Zenaida galapagoensis*)."

Charles Walcott, Laboratory of Ornithology, Cornell Univ., Ithaca, NY 14850, "Cues homing pigeons use for orientation may vary on loft location."

Brad Andres, Dept. Zoology, Ohio State Univ., Columbus, OH 43210, "The hyperphagic race: patterns of arctic shorebirds."

Stephen Flemming, Queen's Univ., Kingston, ON, Canada, "Social foraging by Ospreys: local enhancement and the use of risk-averse flocking."

James L. Ingold, Franklin and Marshall College, Lancaster, PA 17604, and James E. Jurgenson, Jeffrey B. Stunt, and Susan Colilla, Dickenson College, Carlisle, PA 17013, "Restriction fragment length polymorphisms of Ruby-crowned and Golden-crowned Kinglet mitochondria."

Robert J. Craig, Univ. Connecticut, Storrs, CT 06269-4087, "Ecological and morphological divergence in a Pacific island Reed Warbler."

Lynn A. Mahaffy, Dept. Natural Resources, Cornell Univ., Ithaca, NY 14853, "Water off a duck's back: is feather structure a key to water-repellency?"

J. D. Rising, Karen Haberman, and D. I. MacKenzie, Univ. Toronto, Toronto, ON, M5S 1A1, Canada, "Geographic variation in the Gray Kingbird (*Tyrannus dominicensis*)."

Richard C. Banks and M. Ralph Browning, U.S. Fish & Wildl. Service, National Museum of Natural History, Washington, DC 20560, "Nagging questions about the status of Thayer's Gull."

Nancy Dwyer, Univ. Florida, Gainesville, FL 32611, "Florida Sandhill Crane nest-site selection."

David E. Blockstein, A.I.B.S., Washington, DC 20001-4521, "The endangered Grenada Dove (*Leptotila wellsi*): a status update."

Richard N. Conner and D. Craig Rudolph, Southern Forest Experiment Station, U.S. Forest Service, Nacogdoches, TX 75962, "Forest fragmentation and small Red-cockaded Woodpecker populations."

Derek W. Stinson, Div. Fish & Wildlife, Saipan, CNMI, 96950, "The Mariana Common Moorhen: decline of an island endemic."

Joseph M. Wunderle, Instit. Tropical Forestry, Rio Piedras, PR 00928-2500, "The effect of hurricane Hugo on bird populations in a Puerto Rican rainforest."

Jon C. Barlow, Dept. Ornithology, Royal Ont. Mus., Toronto, ON, M5S 2C6, Canada, "Does the Tropical Mockingbird (*Mimus gilvus magnirostris*) of St. Andrew Island mimic?"

Anthony L. Lang, Dept. Zoology, Univ. Toronto, Toronto, ON, M5S 1A1, Canada, "Patterns of geographic variation of song populations of the Eurasian Tree Sparrow."

Ernest J. Willoughby and Marie Cox, St. Mary's College of Maryland, St. Mary's City, MD 20686, "Calls of the Chipping Sparrow."

Russell C. Titus and Carola A. Haas, Dept. Natural Resources, Cornell Univ., Ithaca, NY 14853, "Singing behavior of American Robins."

John M. Hagan, III, J. Michael Reed, Elizabeth A. Cromie, and Roger E. Frost, Manomet Bird Observatory, Manomet, MA 02345, "Environmental sources of selection on songs of North American warblers."

Jonathan L. Atwood, Mark J. Kasprzyk, Trevor L. Lloyd-Evans, Simon P. Barrette, M. Kathleen Jensen, and Danielle M. Stearns, "Aerial mist-netting in a deciduous tropical forest."

David E. Blockstein, A.I.B.S., Washington, DC 20001-4521, "Proposed federal legislation to conserve biodiversity."

Edward H. Burtt, Jr., Dept. Zoology, Ohio Wesleyan Univ., Delaware, OH 43015, "Energy correlated changes in feeding postures of Parids."

Gonzalo Castro, Dept. Biology, Colorado State Univ., Fort Collins, CO 80523 and National Ecol. Res. Center, U.S. Fish & Wildl. Service, 4512 McMurray Ave., Fort Collins, CO 80525-3400, "Use of electrical conductivity to estimate body fat in live birds."

Erica H. Dunn and Diane L. Tessaglia, Laboratory of Ornithology, Cornell Univ., Ithaca, NY 14850, "Project Feederwatch: monitoring winter bird populations at North American feeders."

Walter G. Ellison, Dept. Ecology and Evol. Biol., U-43, Univ. Connecticut, Storrs, CT 06269, "Patterns of vagrancy by Blue-gray Gnatcatchers in New England from 1937–60."

Peggy Ferebee and H. T. Hendrickson, Univ. North Carolina at Greensboro, Greensboro, NC 27412, "Forty-year population trends of selected wintering passerines in piedmont North Carolina."

Jeremy A. T. Hussell, Aurora, ON, L4G 2B1, Canada, and Erica H. Dunn, Laboratory

of Ornithology, Cornell Univ., Ithaca, NY 14850, "Goldfinch preferences for location of bird feeders."

Susannah K. Graedel, New Jersey Audubon Soc., Bernardsville, NJ 07924, "Diurnal and seasonal mass variation in winter resident birds."

Vincent N. LaPolla, Miami Univ., Oxford, OH 45056, "Biculture stripcropping: effects on avian diversity and abundance."

Richard A. Lent, Seatuck Res. Program, Islip, NY and Dept. Ecol. and Evol., SUNY Stony Brook, NY 11790, "Reproductive success and density of Gray Catbirds: Scale effects."

James D. Lowe and Gregory S. Butcher, Laboratory of Ornithology, Cornell Univ., Ithaca, NY 14850, "Population dynamics of the Loggerhead Shrike (*Lanius ludovicianus*) in winter (1963–1987)."

Gail P. Senesac and Gregory S. Butcher, Laboratory of Ornithology, Cornell Univ., Ithaca, NY 14850, "Reproductive success of Eastern Bluebirds (*Sialia sialis*) in agricultural habitats."

Diane L. Tessaglia and Erica H. Dunn, Laboratory of Ornithology, Cornell Univ., Ithaca, NY 14850, "Using Project Feederwatch data to detect seasonal movements and abundance of Pine Siskins (*Carduelis pinus*)."

F. E. Wasserman and J. Cigliano, Dept. Biology, Boston Univ., Boston, MA 02215, "The interaction between song length and song rate in stimulating female White-throated Sparrows."

ATTENDANCE

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CONNECTICUT: *Hadlyme,* Jule Zickefosse; *Litchfield,* Gordon Loery; *Lyme,* Ginger Bladen; *New Haven,* Bryon G. Butler, Patricia Noyes, Fred C. and Margaret Sibley; *Storrs,* Winifred B. Burkett, George A. Clark, Jr., Robert Craig; *Willimantic,* Tom Harrington.

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